THE FOSSIL RECORD OF *ELAEOCARPUS* L. FRUITS

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Elaeocarpus L. fruit stones from Australian mid-Tertiary sediments are systematically described and their stratigraphic and geographic distributions recorded. The fossil fruit stones comprise 2-9-loculate inner mesocarps, their outer surface with longitudinal sutures and a sculpture ranging from smooth to pitted, baculate/verrucate/echinate/rugulate, or fossulate. The fertile locules have a near apical seed and the seedless locules are usually compressed; thin-walled endocarps dehisce loculicidally and enclose the locules. The seed coat is bitegmic and has a multiplicative tegmen, the outer epidermis of which comprises thick-walled, pitted sclereids. Five types of fruit stones are distinguished on the basis of their surficial sculpture. Types 1 and 2 have verrucate/rugulate surfaces, Type 1 being distinguished by a higher ratio (>0.1) of sculptural base diameter:transverse diameter of fruit stone than that of (<0.1) Type 2 fruit stones. Types 3, 4, and 5 have pitted, smooth, and fossulate surfaces respectively.

A review of fossil fruit stones attributed to *Penteune* F.Muell., 1874, *Pleiocliuis* F.Muell., 1882, *Phymatocaryon* F.Muell., 1871, and *Rhytidotheca* F.Muell., 1871 confirms these categories are congeneric with *Elaeocarpus*. One new species, *E. rozefeldsii*, is proposed and type specimens are designated for *E. allportii* (F.Muell.) comb. nov., *E. angularis* (F.Muell.) Selling, 1950, *E. bivalve* (F.Muell.) comb. nov., *E. brachyclinis* (F.Muell.) comb. nov., *E. couchmanii* (F.Muell.) comb. nov., *E. johnstonii* (F.Muell.) comb. nov. (and its junior synonym, *E. bassii* Ettingsh.), *E. lynchii* (F.Muell.) Selling, 1950, *E. muelleri* Ettingsh., 1886, *E. pleioclinis* (F.Muell.) comb. nov., and *E. trachyclinis* (F.Muell.) Selling, 1950.

The fossil fruit stone record confirms that *Elaeocarpus* was represented in the eastern Australian flora as early as the Early Oligocene. Modifications to the distribution range and diversity levels of the genus have occurred in eastern Australia since the Neogene. These involved the loss of taxa with Type 5 stones from Australia and a shift to more northerly areas of eastern Australia of species groups with Types 2, 3, and 4 fruit stones. □ *Elaeocarpus, fossil fruit stones, Australia, mid-Tertiary.*

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Elaeocarpus L., a genus of ~ 60 or 360 species (Mabberley, 1987) occurring in tropical and warm regions of the Old World excluding Africa has an extensive fossil record from Tertiary sediments of eastern Australia. The fossil taxa are leaf remains that include compressions, impressions and cuticles (Ettingshausen, 1883; 1886; Christophel, 1994; Carpenter et al., 1994) and fruits that occur as permineralised casts and moulds or charcoalified compressions (Mueller, 1871a,b, 1873, 1874a,b, 1878, 1882; Johnston, 1880a,b, 1882; Ettingshausen 1883, 1886; Deane, 1925; Berry, 1926; Kirchheimer, 1935; Selling, 1950; Rozefelds, 1990; Rozefelds & Christophel, 1996a, b, in press; Burrows, 1997). *Elaeocarpus*-type pollen has been recorded extensively from eastern Australian sediments of late Eocene-Recent age (Luly et al., 1980; Truswell et al., 1987; Kershaw et al., 1994; Blackburn & Sluiter, 1994; Martin, 1998) but the small, psilate, tricolporate pollen are difficult to discriminate from those of certain other Elaeocarpaceae (e.g. *Sloanea*) and Cunoniaceae, and detailed comparative studies on pollen of the two families are not available.

The present paper incorporates a taxonomic account of fossil *Elaeocarpus* fruit taxa reported from Australia, and documents their known geographic and stratigraphic distributions. Eighteen species of fossil fruits referable to *Elaeocarpus* have been reported from mid-Late Cainozoic sediments of eastern Australia, and one is newly described herein.

STUDIES ON FOSSIL FRUITS OF *ELAEOCARPUS*

In 1883 Ettingshausen described fossil fruits from Tasmania under the name *Elaeocarpus bassii* and was thus the first to attribute fossil fruits to the genus from the Australian Tertiary.

However, the earliest reference to fossil fruits consistent with those of *Elaeocarpus* dates from Mueller & Smyth's (1870:390) reference to a 'five valved capsule of an unknown genus' recovered from deep lead sediments at Haddon, Victoria. Specimens answering to that description were subsequently attributed to *Penteune*, which name is 'an allusion to the five valves in which the seeds are imbedded' (Mueller, 1874a: 41). Mueller is the author of 10 other fossil fruit species consistent with *Elaeocarpus* and instituted (1871a,b, 1874a, 1882) *Rhytidotheca, Phymatocaryon, Penteune* and *Pleioclinis*, to accommodate them. *Pleioclinis* was first used without a description or illustration in a note accompanying the description of *Rhytidotheca pleioclinis* (Mueller, 1873), and was formally described later (Mueller, 1882).

Mueller's generic diagnoses must be treated with caution for they do not always comply with the characters displayed by the species he attributed to them. For instance, *Penteune* was proposed for fruits with surface sculpture 'very slightly rough on the dorsal part' (Mueller, 1874a: 41), but on the same page, *P. trachyclinis*, is described as 'externally very rough, almost verrucular'. For *Pleioclinis* seed placentation was diagnosed as pendent (Mueller, 1882: 43), but in *Rhytidotheca pleioclinis* F. Muell., which was later transferred to *Pleioclinis* (Mueller, 1882), the seeds are said to be erect. Furthermore, fruit-valve number, a character that initially discriminated the genera, was later found to be variable; original diagnoses were not emended.

Mueller had difficulty in discriminating between his genera. For instance, he (Mueller, 1874b: 42) emphasised the sculptural similarity between the 5-valved *Penteune trachyclinis* and the 2-4 valved *Phymatocaryon mackayi*, but later (Mueller, 1875: 41) reported that fruits of *P. trachyclinis* with 4 valves bore much resemblance to *P. mackayi*. Subsequently, he (Mueller, 1882: 43) observed that *P. trachyclinis*

resembled rare 5-valved specimens of *Pleioclinis couchmanii*, the diagnosis of which specified 7-9, rarely 6 valves. It is also likely that Mueller had doubts that *Penteune* and *Rhytidotheca* were discrete genera as he noted for *Penteune clarkei* that 'some affinity of these fossils to those of the genus *Rhytidotheca* is evident (Mueller, 1874b: 41). Thus, over 8 years Mueller directly or indirectly interlinked *Rhytidotheca, Penteune, Phymatocaryon* and *Pleioclinis* all of which are here associated with *Elaeocarpus* (Table 1).

Because Mueller possessed so wide a knowledge of the Australian Flora it is of interest to speculate as to why he created these 4 fossil genera. In discussions accompanying the generic descriptions, Mueller made it clear he was of the opinion that it was improper to assign fragmentary fossil material to extant genera. However, for *Penteune, Phymatocaryon* and *Rhytidotheca* he suggested affinities with Sapindaceae amongst living taxa thereby strengthening the view the fossil genera were related. His reasons for selecting the Sapindaceae are spelled out in the discussion accompanying the description of *Phymatocaryon* (Mueller, 1871a: 47). There he noted that the pendent seeds, locular dehiscence, drupaceous fruits ('with a distinct sarcocarp and putamen') are all family characters of the Sapindaceae. Furthermore, he observed that the fruits of some members of the family also have surfaces that exhibit 'tubercular roughness'. He may have been particularly swayed by this character since 5 years earlier he had described *Cupaniopsis tomentella* (F.Muell. ex Benth.) S.Reyn., fruits of which are described by Reynolds (1985) as 'valves, thick rugose, deeply wrinkled outside'.

Nonetheless Mueller was not entirely satisfied his fossil fruit genera all belonged in the Sapindaceae for a few months later he noted the similarity of *Rhytidotheca* to the fruits of *Flindersia* and *Chloroxylon* (Mueller, 1871b: 39) then placed in the Meliaceae. He discounted an

TABLE 1. The three principal characters stressed by Mueller in his original diagnoses of fossil fruit genera now associated with *Elaeocarpus.* Bracketed valve numbers designate the less common state(s); bracketed shape and sculptural designations comply with terminology used herein.

Genus	Valve number	Shape	Surface
Penteune	(4) 5 (6)	Ovate-globose to broadly ovate (spherical-prolate ellipsoidal)	Slightly rough-deeply wrinkled (pitted-verrucate/rugulate)
Rhytidotheca	5	Ovate (perprolate ellipsoidal)	Wrinkled (rugulate)
Phymatocaryon	2-3 (4)	Spherical to ovate (spherical-prolate)	Rough-deeply wrinkled (baculate/verrucate-rugulate)
Pleioclinis	(5-6) 7-9	Ovate globular-ovate (spherical-prolate)	Tubercular-rough (verrucate-rugulate)

affinity with the Sapindaceae because 'the number of fruit-valves, increased to five, remains exceptional'. Though most Sapindaceae have 3-loculate fruits there are many with fewer or more carpels and so it is surprising Mueller was so concerned on that account. Likewise, in his discussion of the affinities of *Penteune* he wrote, 'It belonged, however, most probably to Sapindaceae, although the possibility of it having formed a genus of the meliaceous order is not excluded' (Mueller, 1874a: 41).

Why Mueller failed to recognise the similarity of at least *Penteune* with fruits of *Elaeocarpus* is difficult to understand unless it stemmed from him being familiar, as is likely, only with fresh material that had been pressed or stored in preservative. In these circumstances the fruit stones do not disintegrate. They do so after prolonged exposure to wet/dry weathering cycles and/or degradation by fungi and/or insect attack. Under these circumstances disintegration of the stony mesocarp into segments may occur after loss of vascular tissue from the central cylinder and the radial strands that connect the central cylinder to the segment sutures. It is likely that fossil fruits were subjected to similar degradation processes during incorporation into sediments. Moreover, many of those from deep lead sediments have been pyritised, and oxidation after recovery and storage may cause the mesocarp segments to separate. Thus, Mueller was very likely distracted from the real identity of the fossil fruits because many dehisced into segments as a result of burial, fossilisation, and subsequent retrieval and storage.

By 1884 Mueller was aware that *Rhytidotheca* fruits were considered consistent with those of *Elaeocarpus* because *R. johnstonii* F.Muell.(in Johnston, 1882) was based on material assigned by Ettingshausen (1883) to *E. bassii* Ettingsh. Nonetheless, he did not comment on or challenge Ettingshausen's assignment. Likewise it is surprising that Ettingshausen (1883: 63), having recognised that *E. bassii* and *R. johnstonii* were conspecific, relegated other species of *Rhytidotheca* (*R. lynchii*, *R. pleioclinis*) to *Incertae sedis* without comment. Furthermore, he did not suggest that *Penteune* and *Elaeocarpus* might be congeneric and followed Mueller in assigning the former to Sapindaceae (Ettingshausen,1883:16) rather than Tiliaceae in which at that time *Elaeocarpus* was included. In a lecture to the Royal Society of Tasmania, Mueller (1884) restated his argument (Mueller, 1871a) for not including fossil leaves and other plant organs in extant genera.

The likely affinity of *Phymatocaryon mackayii* F.Muell., 1871 with *Elaeocarpus* was noted by Deane (1925) and confirmed by Kirchheimer (1935) after detailed comparison of fossils and mesocarps of extant *E. angustifolius*. Selling (1950) formally transferred several of Mueller's species to *Elaeocarpus* without comment. As noted by Selling (1950) transfer of *Rhytidotheca lynchii*, *Penteune clarkei*, *P. allportii*, *P. brachyclinis*, and *P. trachyclinis* to *Elaeocarpus* rendered *Penteune* and *Rhytidotheca* superfluous. Rozefelds (1990) and Rozefelds & Christophel (1996a, b; in press) provided evidence for reference of several fossil fruit taxa to *Elaeocarpus*. These include *E. clarkei*, *E. spackmaniorum*, *E. cunningii*, and *E. mackayii*. However, they expressed doubts about a relationship, as suggested by Selling (1950), of *Rhytidotheca lynchii*, *Penteune trachyclinis*, and *Phymatocaryon angulare* with *Elaeocarpus*.

MATERIAL

Fruits reported upon here include charcoalified material from subsurface sediments near Moranbah and Blackwater in central Queensland and permineralised material from Glencoe (Rozefelds, 1990; Rozefelds & Christophel, 1996b, in press) that are held in the Queensland Museum (QMF); charcoalified and lignified fruits in the Australian Museum (AMF), the Department of Mines, Geological Survey of New South Wales (MMF), and the Museum of Victoria (NMVP). The last mentioned collection includes most of Mueller's Victorian material originally housed in the Geological Survey of Victoria. Mueller's material came from deep lead sediments in Victoria and New South Wales and specimens illustrated by Mueller have been identified for most of his Victorian species. Mueller's New South Wales material may have been destroyed in the Garden Palace fire in 1882 which included 'the palaeontological specimens of the recently deceased Reverend W.B. Clarke' (Gilbert, 1986: 107). Clarke collected several of the fruits described by Mueller from New South Wales. The repository of type material of *E. muelleri* Ettingshausen, 1886 is also unknown. Tasmanian material attributed to *E. bassii* by Ettingshausen (1883) and to *Penteune allportii* and *Rhytidotheca johnstonii* by Mueller (in Johnston, 1882) has not been located. Other material not examined includes *Rhytidotheca major* Deane, 1925 and *E. cerebriformis* Rozefelds & Christophel, 1996b.

LOCALITIES. (Fig. 1).

Queensland. a) Picardy Station, near Moranbah 21°5'17.6"S 147°50'34.3"E. Holes RDPD98MA 17, 111-133m and RDPD98MA21, 123-133m. Fruits were recovered from both boreholes from near the base of a thin sequence of sands and silts with interbeds of lignites that occur beneath basalts and overlie Permian Coal Measures (Fig. 2A). The basalts are probably related to those of the Nebo Province dated as 30-34 Ma. (Wellman & McDougal, 1974, Sutherland pers. comm.), but stratigraphic relationships between these and those intersected in the boreholes have not been established. Host sediment was not retained for palynological assessment. Thus, the minimum age is tentatively suggested as Early Oligocene.

b) Near Blackwater 24°1'1.3"S 148°48'50"E. South Blackwater Coal Pty Ltd Hole R8736, 82m. Fruits are from ligneous bands within sands that underlie basalts and overlie Permian sediments (Fig. 2B). Basalts to the SW in the Springsure area are dated at 27-33Ma. (Sutherland et al., 1977), but stratigraphic relationships between dated basalts and those in borehole R8736 are uncertain. Moreover, no sediment was available for palynological analysis and a minimum age of Early-Late Oligocene is tentatively indicated.

e) Glencoe Station (23°36'S 148°06'E), near Capella (Rozefelds, 1990; Rozefelds & Christophel, 1996a, in press). These occur in silcretes that overlie undated basalts. However, volcanics near Emerald are dated as 30-32Ma. and those southwest of Capella at 26Ma. imply a maximum Oligocene age, possibly Late Oligocene-Early Miocene according to Rozefelds (1990).

New South Wales. Elaeocarpus-type fruits are known from a scatter of localities on the western flanks of the eastern highlands of northern and central New South Wales (Fig. 1).

a) Newstead near Elsmore (29°47'S, 151°17'E), Ettingshausen (1886) described *E. muelleri* fruits from ironstones overlain by basalts. Piekett et al. (1990) concluded an Early Miocene or younger age based on K-Ar dates of 20.5 ± 0.2Ma. for a nearby basalt flow.

b) At Witherden's Tunnel, near Emmaville leaf fossils attributed to *E. muelleri* were recorded from carbonaceous clays and silts beneath basalts (30.4 ± 0.3Ma.); palynological dates confirm a Late Eocene age (Pickett et al., 1990). However, there is no evidence to suggest that the leaf and

1	Picardy Station
2	Glencoe Station
3	Blackwater
4	Elsmore
5	Gulgong
6	Dubbo
7	Orange
8	Bathurst
9	Carcoar
10	Eldorado
11	Talbott
12	Guildford
13	Boola Boola
14	Foster
15	Tanjil
16	Yallourn
17	Haddon
18	Beaconsfield
19	Launceston
20	Geilston Bay
21	Bethany

FIG. 1. Map of Australia showing localities from which fossil fruits of *Elaeocarpus* have been reported.

mesocarp fossils from the separate localities derived from the same plant taxon.

c) Gulgong district (32°12'S, 149°32'E) sites include Home Rule Lead and Black Lead (Mueller, 1876, 1877, 1879). The leads are sediment fills of palaeodrainage channels on Palaeozoic basement and are overlain by basalt flows. Isotope ages (K-Ar) of the basalts range from 13.8 ± 1.2Ma to 14.8 ± 1.2Ma. (Dulhunty, 1971; Meakin & Morgan, 1999). The Home Rule Lead is assigned to the Middle Miocene *Triporopollenites bellus* Zone (McMinn, 1981) in agreement with isotope dates.

d) At Orange (33°17'S, 149°06'E), Carcoar (33°37'S, 149°08'E), and Bathurst (33°25'S, 149°35'E) charcoalified fruits are known from beneath basalts in numerous deep leads and reef mines. As at Gulgong the sediments are overlain
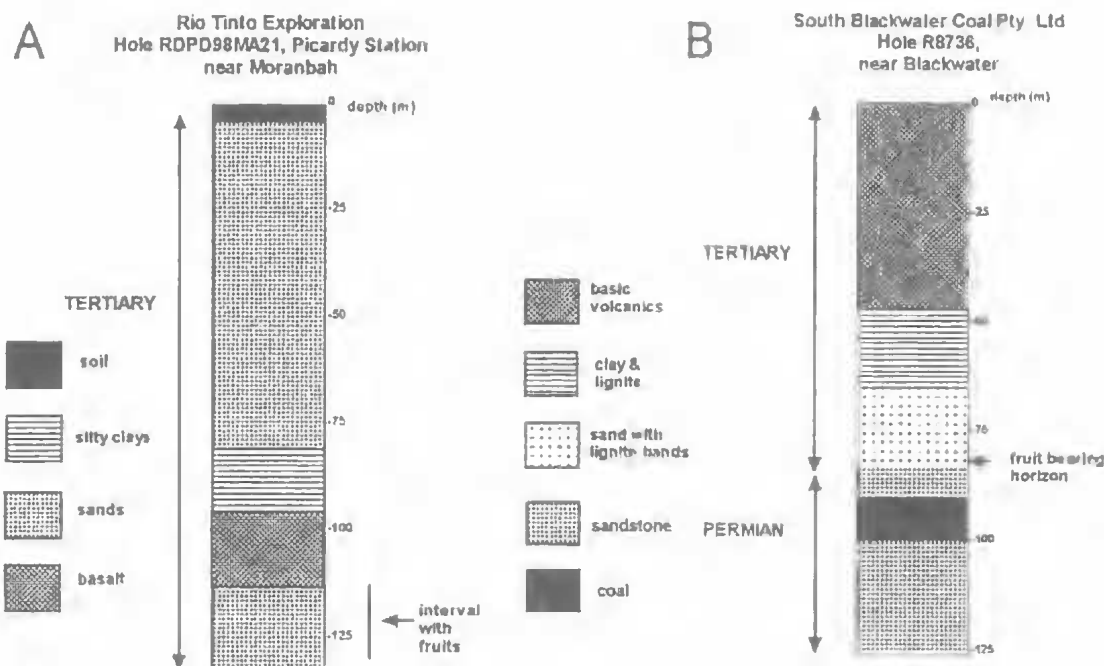
FIG. 2. Stratigraphic sequences and sampling horizons in: A, Hole RDPD998MA17, Picardy Station near Moranbah, Queensland; and B, South Blackwater Coal Pty Ltd Hole R8736 near Blackwater, Queensland.

by basalts that were extruded from Mt. Canabolos SW of Orange. Basalts that overlie the sediments at Forest Reefs and in the Lucknow Mine have provided dates of 11.2-13Ma., late Middle-early Late Miocene (Johnson, 1989).

Victoria. Fossil fruits have been collected from buried placer deposits in the Murray, Gippsland and Otway Basins, and on the northern flanks of the Great Divide. There are few data on precise ages of the deep lead sediments.

a) The Eldorado deep lead (Ted Ovens G & TM Co. Shaft), Beechworth (37°18'S 146°32'E), in the Murray Basin, (Mueller, 1874c: fig. 2) is of unknown age. Palynological dates on other Murray Basin deep leads near Stawell, W Victoria and in the Woodstock 10008 bore near Bendigo, Victoria, indicate Oligocene and late Early Miocene ages based on reference of the former to the lower *Proteacidites tuberculatus* spore-pollen Zone and of the latter to the upper part of that zone (Partridge & Wilkinson, 1982; Partridge, 1993).

b) The bulk of fruits described by Mueller were obtained from deep lead sediments at Smythe's Creek (Reform Co. Shaft) and Nintingbool (Crucible Co. Shaft), near Haddon (37°18'S 146°32'E), SW of Ballarat. Silty sands of the 'wash dirt' overlying basement near the bottom of the shafts (Reform Co. Shaft, ~47.5m (156ft);

Crucible Co. Shaft, ~23.2m (76ft)) are designated as the source of the fruits (Mueller, 1874c: 29, Map 1), and in the Reform Shaft the sediments are beneath basalts. Dates of 2-5Ma. have been obtained from basalts that overlie alluvial sediments in the Ballarat district (Sutherland, 1995) and palynofloras recovered from sediments intercalated between two of the flows indicate the *Tubulifloridites pleistocenicus* spore-pollen Zone of late Pliocene to Pleistocene age (Partridge, 1995). The minimum age of the subbasaltic sediments is thus Late Miocene age, but Rozefelds & Christophel (1996b) argue for an Early-Middle Miocene age based on association of the fruit *E. mackayii* (F.Muell.) Kirchheimer, *E. clarkei* (F.Muell.) Selling, and *Spondylostrobus smythii* F.Muell. (see also Greenwood et al., 2000). Unfortunately, Mueller did not always specify precise depth or mine shaft for localities at Haddon.

c) Gippsland Basin deep lead sediments at Talbot (37°10'S 146°14'E), Foster (37°10'S 146°14'E) and Tanjil (38°01'S 146°14'E). Thus far, the ages of these have not been resolved, but as for the Haddon sediments Rozefelds & Christophel (1996b) suggest an Early-Middle Miocene age.
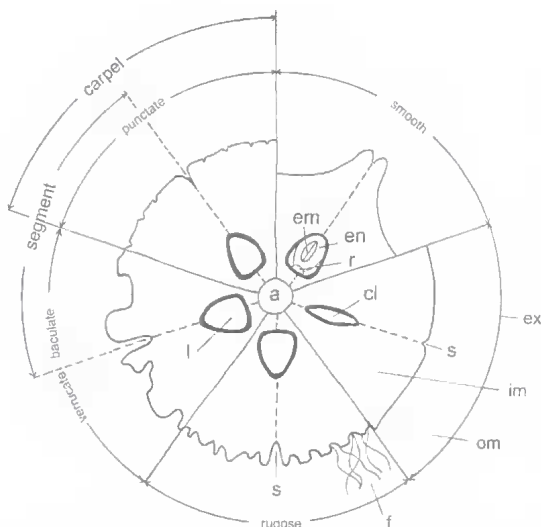
FIG. 3. Stylised transverse section of *Elaeocarpus* fruit in which each of the 5 carpels has different surfical sculpture of the inner mesocarp. a, axis; cl, compressed locule; e, endocarp; en, endosperm; em, embryo; ex, exocarp; f, fibres; im, inner mesocarp; om, outer mesocarp; l, locule; r, raphe; s, suture.

d) Yallourn Coal Measures, Yallourn (38°10'S 146°21'E) in the Yallourn Formation whithin the *Triporopollenites bellus* spore-pollen Zone of late Early-Late Miocene age (Rozefelds & Christophel, 1996b).

South Australia. Fruits from subsurface sediments near Bethany (34°32'S 139°00'E) in the Barossa Basin (Paterson in Hossfeld, 1949) occur in the Rowland Flat Sand, a lignitic facies overlain by coarse-grained fluviolacustrine sand and gravel fining upwards to bedded silt and clay. Palynological dates are Early Oligocene-Early Miocene for the basal sediments and Early-Late Miocene for coarser upper facies (Alley, 1995).

Tasmania. Deep lead sediments at Brandy Creek, Beaconsfield (41°12'S 148°49'E) and outcrops at Launceston (41°27'S 147°10'E). A mid-Tertiary (Oligocene) age is indicated for these localities based on palynofloras of sub-basaltic sediments in the Tamar Graben (Forsyth, 1989).

b) Calcareous fruits from Geilston Bay, Hobart (41°12'S 148°49'E) occur in travertine which is equivalent in age to nearby basalts dated as 22.4 Ma, Early Miocene (Tedford et al., 1975).

New Zealand. a) At Mangonui (35°00'S 173°20'24"E), north of Auckland, charcoalfied fruits occur Mangonui Formation lignites (Late Miocene) associated with *Cocos zeylandica* Berry (Berry, 1926; Thompson, 1978; Isaac et al. 1994).

b) At Schultz Creek (42°16'48"S 171°07'12"E), north of Greymouth, South Island lake sediments deposited during the last interglacial (100Ka.) have yielded fruits comparable to those of extant *E. dentatus* (Burrows, 1997). The material illustrated has been deposited at the Queensland Herbarium.

METHODS

Charcoalified specimens were photographed after whitening with ammonium chloride; internal characters including those of the locules were photographed without whitening. Mueller's type specimens are figured together with reproduction of the original lithographic illustrations, the latter of which represent mirror images. Available seed coats were examined in transmitted light after clearing in chromium trioxide for several hours, followed by thorough washing in distilled water after which they were mounted on glass microscope slides in glycerine jelly.

Fruit stones of extant *E. angustifolius* Blume and *E. reticulatus* Smith were collected from trees growing at the Brisbane Botanic Gardens, Mt Coot-tha and the University of Queensland.

SYSTEMATIC PALAEOBOTANY

Elaeocarpus L. 1753

Rhytidotheca F.Muell., 1871:39.
Phymatocaryon F.Muell., 1871:41.
Penteune F.Muell., 1874a:3941.
Pleioclinis F.Muell., 1882:43

TYPE SPECIES. *Elaeocarpus serratus* L.

FRUITS OF EXTANT *ELAEOCARPUS*. In extant *Elaeocarpus* fruits develop from flowers with a superior 2-8 (usually 3-5) loculate ovary that terminates in a single style surmounted by a lobed stigma. There are 2-12 anatropous ovules per locule and these are attached to an axile placenta. When there are few ovules per locule they are attached high up on the axis and so appear to be subapical (Figs 4, 6B,C). Only one ovule per locule develops into a seed and in some species there is only 1 seed per fruit. Expansion of this 1 seed usually results in compression of the adjoining seedless locules (Figs 4, 5D,G).

The fruit is a drupe, a useful term, ill-defined but widely used in the literature (Clifford & Dettmann, in press). In most species the fruit surface is iridescent blue, the colour due 'not to a blue pigment, but by the structure of the cuticle which reflects blue light' (Lee, 1991). The outer fleshy mesocarp is usually thin and densely
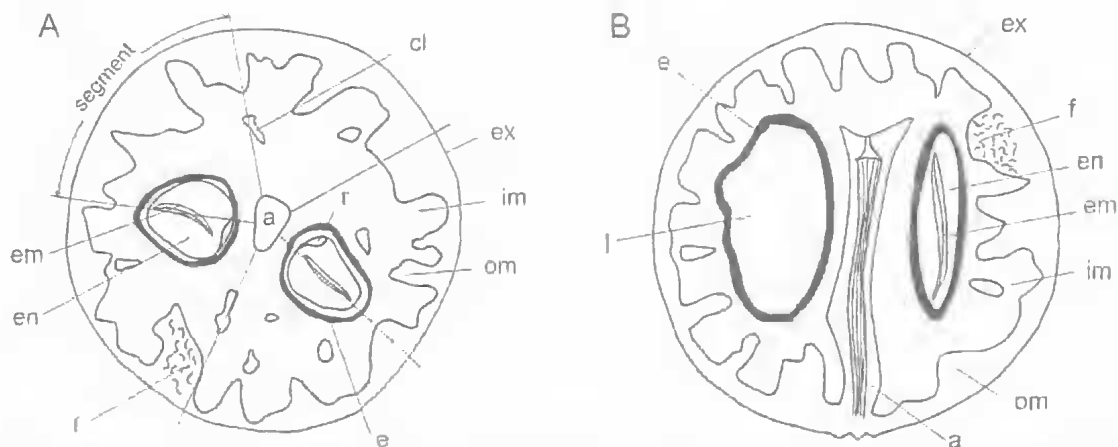
FIG. 4.Sections through *Elaeocarpus angustifolius* Blume fruits: A, transverse; B, vertical. Labels as for Fig. 3.

fibrous, fibres intertwined with the sculptured surface of, or extending into, the woody inner mesocarp (Fig. 5A). The latter encloses the locules and their surrounding endocarps to form a stone whose outer surface may be smooth, pitted, fossulate, rugulate, baculate, verrucate, or echinate. At maturity the vascular strands of the axis decay, resulting in a hollow cylinder which extends for ~ two-thirds the length of the mesocarp from its proximal end (Figs 3, 4, 5F). Further decay of radially disposed strands beneath the segment sutures results in the mesocarp and enclosed endocarps splitting vertically between the septa to produce segments that expose seeds or aborted ovules on their radial walls (Fig 5G-I). As was recognised by Mueller, such dehiscence is loculicidal. The lines along which the mesocarp split are usually clearly marked by vertical sutures on the surface of the mesocarp (Fig. 5A-C) and each segment consists of a woody, inner mesocarp, half of 2 adjacent endocarps and associated locules (Fig. 5H,I). The inner surface of the endocarp may bear multicellular scales and hairs (Corner, 1976).

Seeds are fusiform, bitegmic with glabrous or hairy surfaces. The testa is several cells thick with an outer epidermis of elongate to isodiametric cells (Figs 6I, 7F) that in some species are lignified. The tegmen is multiplicative, the outer epidermis of which has fibriform, bulbous or dumb-bell shaped, lignified sclereids that are arranged longitudinally (Fig. 5G,H). Both the testa and tegmen are vascularised in the chalaza which forms the woody basal and acute prominence of the seed (Corner, 1976).

Shape, structure and surface sculpture of the fruit stones are useful species discriminators

(Rozefelds & Christophel, 1996a). However, such features have been little utilised and remain largely undocumented in current infrageneric classifications. Moreover, little attention has been accorded anatomical features of the inner mesocarp wall and the enclosed endocarps.

The only record of fossil mesocarps attributable to an extant species is that of *E. dentatus* stones in interglacial (100Ka) sediments from New Zealand (Burrows, 1997).

FOSSIL FRUITS. The following fossil taxa are considered congeneric with *Elaeocarpus*.

PENTEUNE F.Muell., 1874; type species (designated here) *Penteune clarkei* F.Muell., 1874a: 41 from Elsmore, NSW; Early Miocene: Neotype (designated Rozefelds & Christophel, 1996a: 43). NMVP53913, Fig. 11A, B;

Mueller's figured specimens from Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5m) are believed lost (Rozefelds & Christophel, 1996a: 43).

Species included: *P. allportii* F.Muell., in Johnston 1882: figs 40, 41, 44-47.*P. brachyclinis* F. Muell., 1874a: 41, pl.8, figs 1-9. *P. trachyclinis* F. Muell., 1874a: 41, pl. 8, figs 10-17.

PHYMATOCARYON F.Muell., 1871; type species*Phymatocaryon mackayi*F.Muell., 1871a. 41 (by monotypy) from Haddon (Smythe's Creek, Reform Co. Shaft, ~47.5m), sediments beneath basalts; ?Early-Middle Miocene;

Lectotype (designated Rozefelds & Christophel (in press)) NMV53562, Mueller 1871a: 41, pl. 2, fig.4:

Species included:*P. angulare* F.Muell., 1874b: 41, pl. 10, figs 1-4. *P. bivalve* F.Muell., 1877: 180, 1878: 39, pl. 15, figs 6-9.
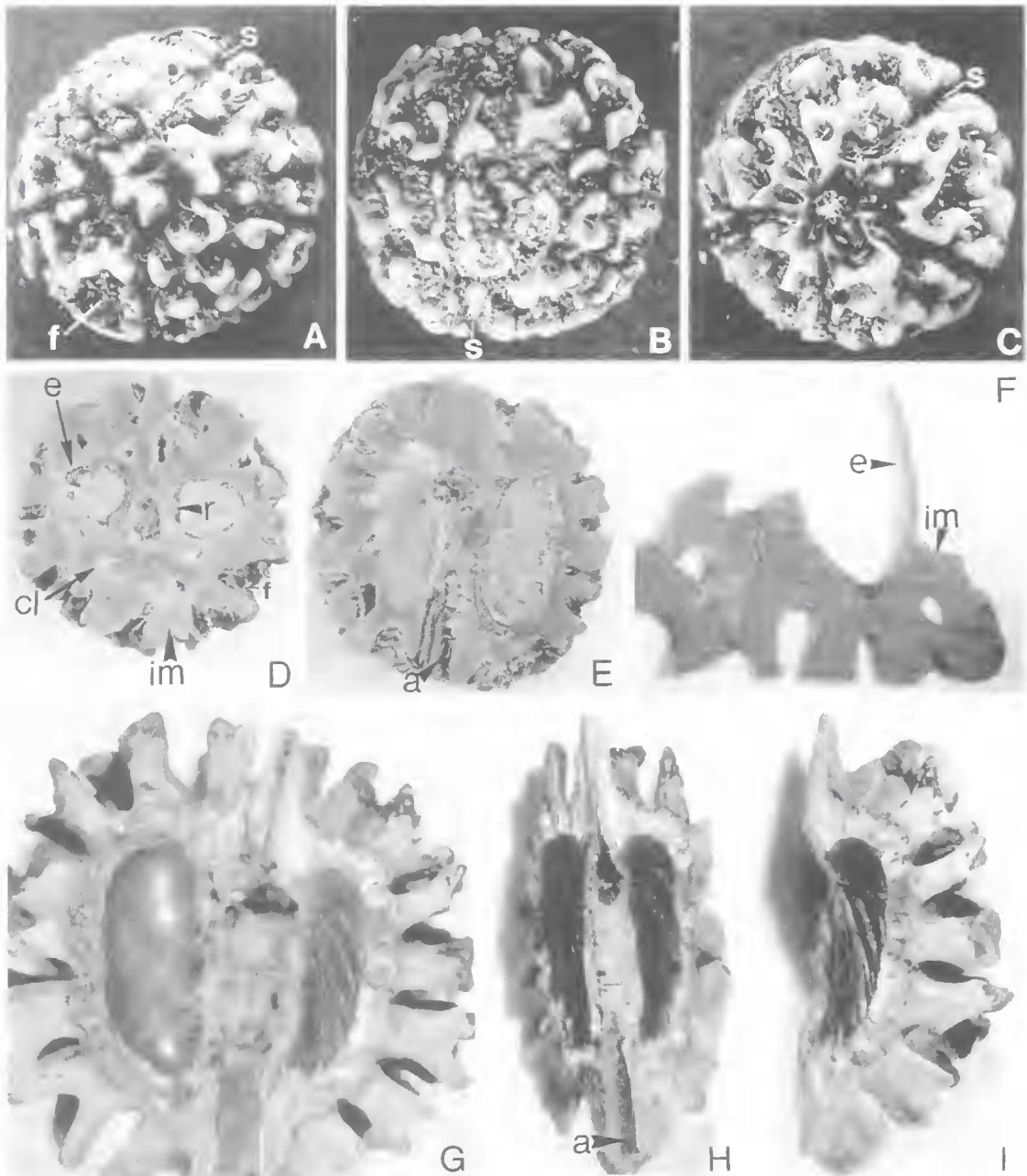
FIG. 5. Fruit stones of *Elaeocarpus angustifolius* Blume. A-C, apical, lateral, and basal views showing sculpture of woody inner mesocarp with attached fibre (f) bundles and sutures, × 2. D, photograph of transverse section in Fig. 4A of fresh, mature fruit stone showing sculptured woody inner mesocarp with fibre (f) bundles on the surface, enclosed endocarps, two with fertile locules containing seeds, each showing the raphe, the other three locules compressed, × 2. E, photograph of vertical section in Fig. 4B showing vascular strands in the axis, × 2. F, vertical section portion of inner mesocarp removed to reveal closely adpressed endocarp, × 4. G, internal view of two segments of partially rotted mature fruit stone showing seed in fertile locule (left), compressed sterile locule (right), and hollow axis, × 4. H, I, internal views of dehisced segment comprising inner mesocarp with halves of two adjacent locules and endocarps showing ridges and grooves on their inner surface, × 4. Labels as for Fig. 3.
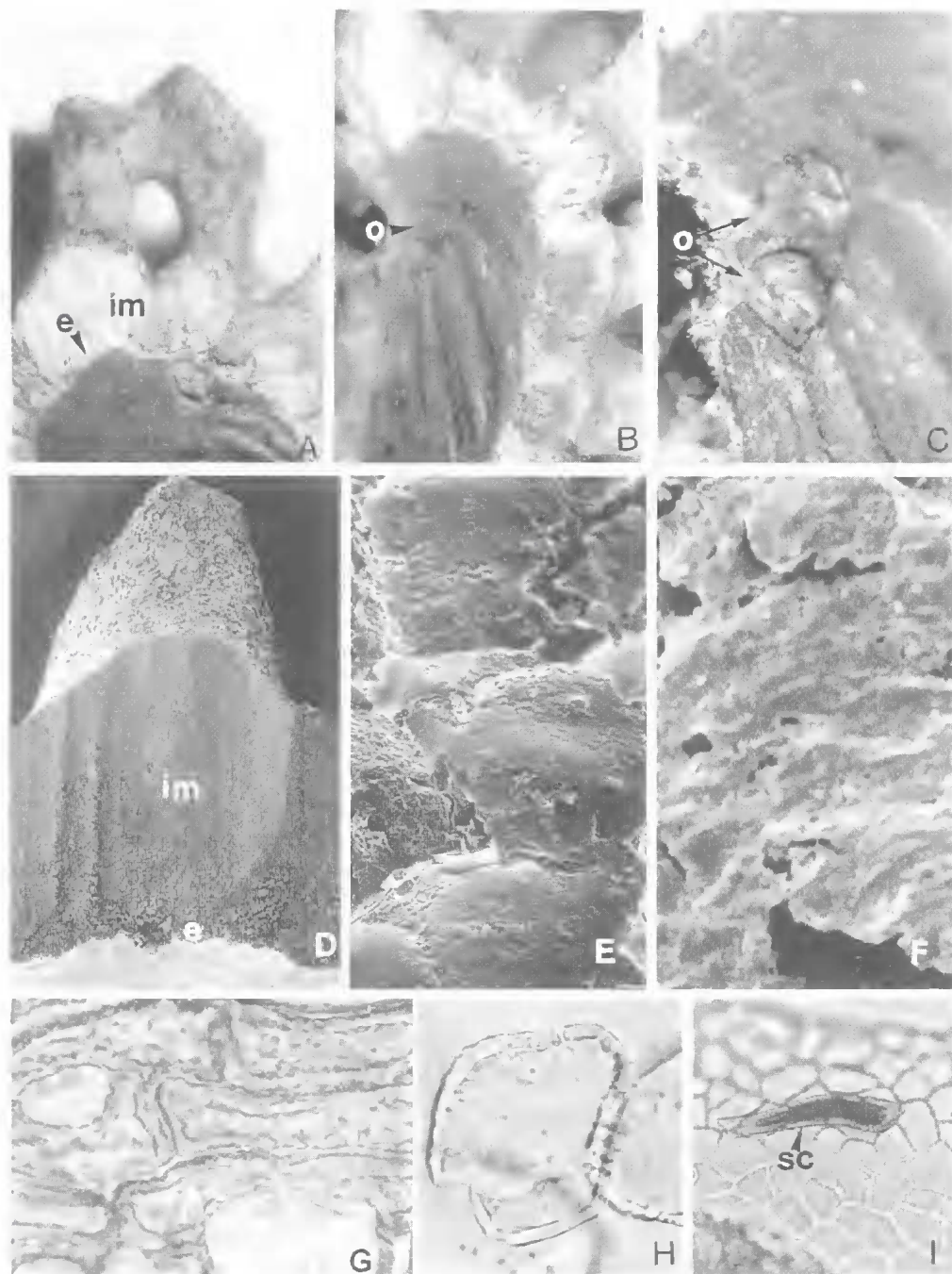
FIG. 6. Micrographs of fruit stones of *Elaeocarpus angustifolius* Blume. A, transverse section of inner mesocarp and endocarp walls, and profile of a concave-crested, arched sculptural element at outer surface of inner mesocarp, × 10. B,C, detail of compressed locule with 2 near-apical, axially attached, aborted ovules (o), and showing coalescence in the apical region of locule of ridges and grooves on inner surface of endocarp, × 10, and × 25 respectively. D, scanning electron micrograph of section of inner mesocarp and endocarp, × 30. E, F, scanning electron micrographs of outer surface and transverse section of inner mesocarp, × 2000 and × 4000 respectively. G, outer epidermis of tegmen showing elongated sclereids with thick, pitted walls, × 750. H, subspherical sclereid from tegmen, × 500. I, outer cuticle of testa, with a sclereid (sc) arrowed derived from outer epidermis of tegmen, × 250. Labels as for Fig. 3.
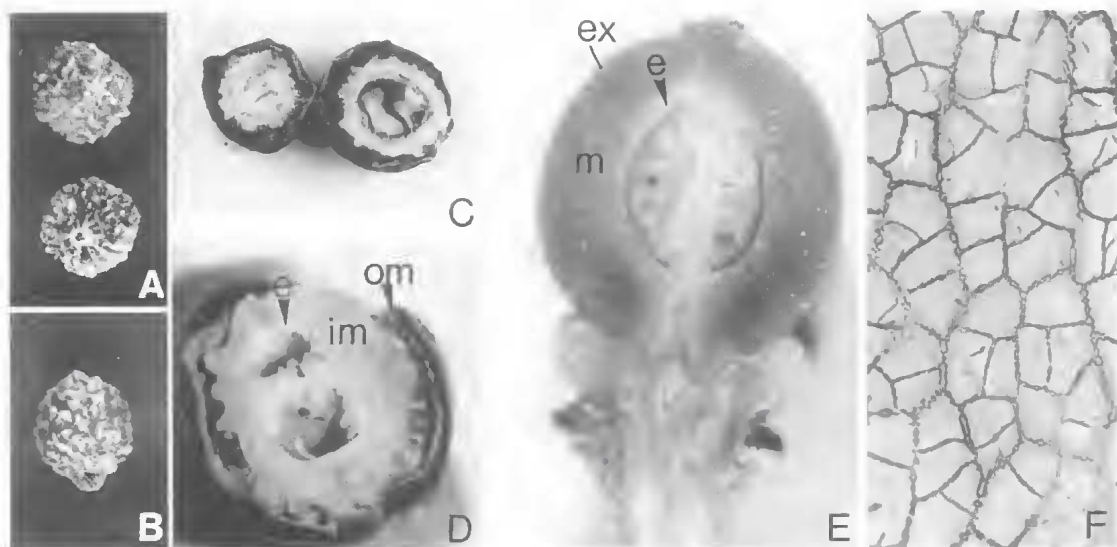
FIG. 7. Fruits, fruit stones and seeds of *Elaeocarpus reticulatus* Smith. A, apical (upper) and basal (lower) views of fruit stone, × 2. B, lateral view of fruit stone, × 2. C, vertical (left) and transverse (right) sections of immature fruits, × 2. D, transverse section of fruit with outer mesocarp partially detached (left) revealing surface sculpture of inner mesocarp, × 6. E, vertical section of immature fruit showing axile placentation and axial tissue, × 16. F, outer cuticle of testa, × 250. Labels as for Fig. 3.

PLEIOCLINIS F.Muell., 1882; type species *Pleioclinis couchmanii* F.Muell., 1882: 43 (by original designation) from Haddon (Smythe's Creek or Nintingbool), sediments beneath basalts; ?Early-Middle Miocene;
Lectotype (here designated). NMVP53920, Mueller 1882: 41; pl. 19, figs 9, 10;
Species included: *Rhytidotheca pleioclinis* F.Muell., 1873), (=*P. shepherdi* F.Muell., 1882; junior objective synonym)

RHYTIDOTHECA F.Muell., 1871; type species *Rhytidotheca lynchii* F.Muell.,1871b:39 (by monotypy) from Haddon (Nintingbool, Crucible Co. Shaft, ~23.2m), deep lead sediments; ?Early -Middle Miocene.
Lectotype (here designated). NMVP6034, Mueller, 1871b:39, pl. 4, fig. 4 (right hand segment) and NMVP6033, Mueller, 1871b: 39, pl. 4, fig. 1, centre segment broken at apex.
Species included:*R. johnstonii* F.Muell.in Johnston, 1882: 50, fig. 6. *R. major* Deane, 1925: 491, pl. 60, fig.12 (nomen nudum). *R. pleioclinis* F.Muell., 1873: 42, pl. 6, figs 1-4.

REMARKS. Recognition of fossilised *Elaeo-carpus* stones has been based on sculpture, shape, locule number, and position of seed attachment (Deane, 1925; Kirchheimer, 1935; Selling, 1950; Rozefelds, 1990; Rozefelds & Christophel, 1996a, b, in press). Woody mesocarps of *Elaeo-*

carpus are distinguished from other Elaeo-carpaceae by: a pitted, smooth, fossulate, verrucate, baculate, echinate or rugose surface with longitudinal sutures that delimit segments; 2-9 carpels; passive loculicidal dehiscence into segments; 1-seeded locules; fertile and sterile locules, the latter often compressed; ovules anatropous, pendulous with a ventral raphe; seeds fusiform with a multiplicative tegmen, the outer epidermis with pitted and lignified longitudinal cells. Further characters with apparent interspecific significance include the internal organisation and structure of the woody inner mesocarp and subjacent locules as revealed by extant *E. angustifolius* and *E. reticulatus* (Figs 5-7). In *E. reticulatus* young fruits have an axial column of elongated vascular strands (Fig. 7E). The inner mesocarp consists of isodiametric stony cells, and the enclosed endocarps comprise lignified cells, elongated and arranged tangent-ially. Fruits of *E. angustifolius* are similar in their organisation (Figs 5,6). Fruit stones allowed to rot on the ground decompose slowly, but after time they may split into segments. Those of *E. angustifolius* were little affected after subjecting them to conditions that may be expected in a medium-high energy depositional situation. Stones agitated with sand, gravel and water in a closed container on a rotary shaker for 1 week showed no signs of breakage or abrasion of the
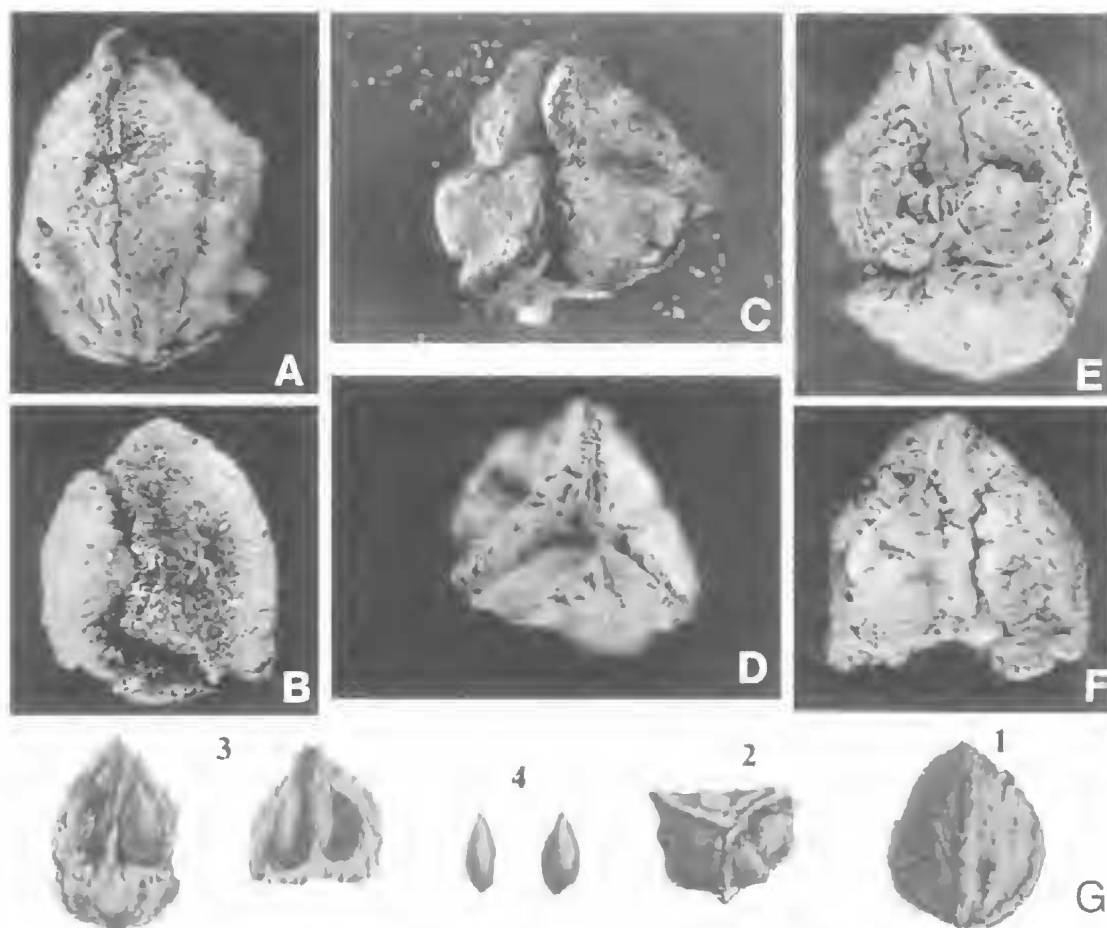
FIG. 8. *Elaeocarpus angularis* (F.Muell.) Selling, fruit stone. A-G, holotype. A, E, lateral views of external and internal surfaces of 2 segments and basal part of third segment (NMVP53565). × 2. B, F, lateral views of external and internal surfaces of upper part of third segment (NMVP6017), × 2. C, D, apical and basal views of whole fruit stone, × 2. G, holotype as illustrated by Mueller (1874b, pl. X, figs. 1-4), but note his images are reversed and seeds represented in his fig. 4 have not been located.

external sculptural elements. However, after drying some dehisced into segments.

Elaeocarpus allportii (F.Muell.) comb. nov.

Penteune allporti F. Muell. in Johnston, 1880a: 27 (nom. nud.).
Penteune allporti F. Muell. in Johnston, 1880b: 85 (nom. nud.).
Penteune allporti F.Muell. in Johnston, 1882: figs 40, 41, 44-47.

MATERIAL. LECTOTYPE (here designated): Whole specimen (Johnston, 1882, figs 40-41) and 4 of its segments (Johnston, 1882, figs 44-47) from Early Miocene Geilston Travertine at Geilston Bay, Tasmania. Stony mesocarp prolate (20mm long, 16mm wide), broadly elliptical in longitudinal section and circular in transverse section; 5-loculate (illustrated as 6-loculate but in

Johnson's Explanation of Figure corrected to 5-loculate). External surface punctate and with 5 longitudinal sutures; preserved mesocarp wall 2-3mm thick. Seed cavity fusoid, apically acute, 14mm long, 5mm wide.

DESCRIPTION. As for lectotype.

REMARKS. No description of calcereous specimens included in the species was provided, but Johnston (1882, Explanation of Figures) illustrated what he believed to be 'probably *P. allporti* F. Muell. F.v.M., *m.s.*' Mueller (1874a: 41) noted, under *Penteune clarkei* F.Muell., that 'an extremely similar fossil has been discovered in Tasmania by Morton Alport (sic), Esq., at Gerlston-Bay (sic) in tertiary travertine'. Selling (1950) suggested inclusion of *P. allportii* in

Elaeocarpus, but did not formally make the transfer.

COMPARISON. May be synonymous with, *E. clarkei* (Johnston,1880b; Mueller, 1874a: 41).

DISTRIBUTION. Geilston Bay, Beaconsfield (Brandy Creek), Tasmania (Johnston 1880a,b, 1882).

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. Possibly with *E. bancroftii* F.Muell. & Bailey.

Elaeocarpus angularis (F.Muell.) Selling, 1950 (Fig. 8A-E)

Phymatocaryon angulare F.Muell. 1874b: 41, pl. 10, figs 1-4.
Elaeocarpus angularis (F.Muell.) Selling 1950: 558.

MATERIAL. HOLOTYPE (by monotypy): NMVP53565 (2 segments plus basal part of third) and NMVP6017 (upper part of third segment) (Fig. 8A-E) from ?Early-Middle Miocene at ~47.5m in Reform Co. Shaft at Smythe's Creek, Haddon, Victoria. Preserved mesocarp ovoid (22mm long, 19mm wide), oval acuminate in longitudinal section and convexly triangular in transverse section; 3-loculate and with 2 equally developed locules exposed, one of which contained a seed now lost. External surface with 3 longitudinal sutures embedded in protruding ridges that extend from base to apex; intervening surface with low relief striations and pits that may be artefacts of abrasion. Mesocarp wall 2-3mm thick with isodiametric cells; endocarp ~0.5mm thick, composed of tangentially aligned cells. Central axis of mesocarp composed of a hollow cylinder of elongated vascular strands that extend from stalk scar to near the apex. Seed cavity fusoid, the apex acute, 10-12mm long, 3-4mm wide. Seeds fragmented, anatomical detail not determined.

DESCRIPTION. As for holotype.

REMARKS. Additional material reported from NSW (Mueller, 1883) has not been located.

COMPARISON. *E. angularis* is similar in size and mesocarp sculpture to *E. (Penteune) brachyclinis*, but was distinguished on its 3 rather than 5 locules (Mueller, 1874b). With 3 locules and position of the seed the taxon was accommodated in *Phymatocaryon* (Mueller, 1874b: 42). *E. (Phymatocaryon) bivalve* was separated from *E. angulare* on its 2 segments (valves sensu Mueller), the edges of which are acute and wing-like and in which the sutures are embedded (Mueller, 1877, 1878). Moreover, in *E. bivalve* 1 of the 2 locules is compressed, unlike *E. angularis*.

DISTRIBUTION. Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5 m), Victoria; Beneree, Dubbo, NSW (Mueller 1874b, 1883).

AGE RANGE. ?Early-Late Miocene.

AFFINITY. As suggested by Selling (1950) with *Elaeocarpus*. However, the lectotype has equally developed locules and the seed coat structure is unknown; an affinity with the Euphorbiaceae is possible (Rozefelds pers. comm.).

Elaeocarpus bivalve (F.Muell.) comb. nov. (Fig. 9A-L)

Phymatocaryon bivalve F.Muell. 1877: 180.
Phymatocaryon bivalve F.Muell.1878: 39, pl. 15, figs 6-9.
Phymatocaryon bivalve F.Muell.1879: 170, pl. 3, fig. 2.
Phymatocaryon bivalve F.Muell. 1883: 9, pl. 15, figs 6-9.

MATERIAL. NEOTYPE (here designated): MMF36220. (Fig. 9A-C) from the late Middle – early Late Miocene Black Lead at Gulgong, NSW. Mesocarp woody, ovoid, vertical axis 17mm, lateral axes 14 and 21mm; with 2 segments delimited by a longitudinal suture and reflexed at their margins; locules 2, one with a near apical seed, the other compressed; dehiscence loculicidal. Mesocarp wall 4mm thick, compact, with a near smooth undulating outer surface. Locules abut the central axis of vascular strands arranged in a hollow cylinder that extends from the stalk scar to near the apex. Endocarp composed of tangentially oriented elements with shortly stalked bifid hairs on the inner surface. Seed cavity ovoid, 10mm long, 4-5mm wide.

DESCRIPTION. Fruit stones woody ovoid, vertical axis 17-20mm, lateral axes 13-16mm and 17-22mm; with 2 segments delimited by flanged and reflexed margins adjacent to the longitudinal sutures; locules 2, one of which is usually compressed, the other with a near apical seed. Mesocarp wall 3.5-6mm thick at segment margin, compact, and with a near smooth undulating outer surface. Locules abut the central axis of vascular strands arranged in a hollow cylinder extending from the stalk scar to near the apex. Endocarp of tangentially oriented elements. Seed cavity ovoid, twice as long as wide; seed with near apical attachment. Seed coat near smooth, testa with outer cuticle of rectangular cells up to 30µm long, 20 µm wide. Tegmen with outer epidermis of elongated, bulbous cells (up to 100µm long, 40µm wide) with pitted, lignified walls 2-4µm thick. Several layers of underlying layers composed of thin-walled (<1µm thick) cuboid cells.

REMARKS. Seed morphology and attachment and seed coat structure of the species is consistent with *Elaeocarpus*. A neotype is designated because the original type series (Mueller 1877, 1878) and those figured by Mueller (1879) have not been located, almost certainly destroyed a century ago. Mueller's specimens illustrated in 1878 have a less prominent flange than those depicted in 1879. New Zealand specimens attributed by Berry (1926) are too abraded for positive identification (Rozefelds, pers. comm.).

COMPARISON. *E. bivalve* is 2-loculate and with imperfect bilateral symmetry with respect to the
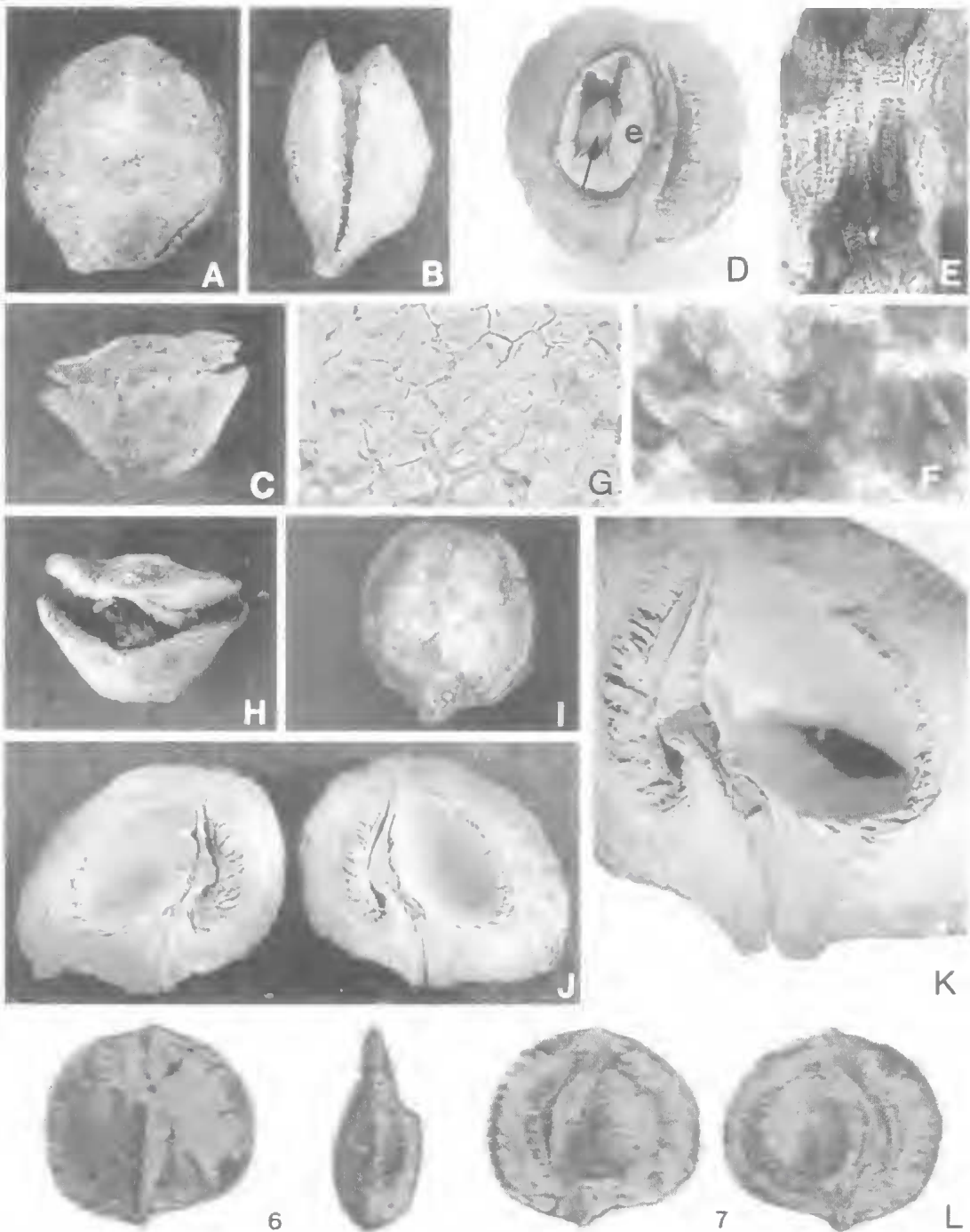
FIG. 9. *Elaeocarpus bivalve* (F.Muell.) comb. nov. fruit stones and seeds. A-C, neotype, × 2, (MMF36220); A,B, lateral view; C, basal views, × 2. D, internal view of segment with one sterile and one fertile locule containing seed (arrow) within endocarp (e), and compressed seedless locule, × 2. E-F, outer epidermis of tegmen of seed illustrated in D showing thick-walled, pitted, bulbous sclereids, × 750, × 250 respectively. G, outer epidermis of testa, × 250, of seed illustrated in D. H, I, fruit stone in apical and lateral views, × 2. J, K, inner surfaces of the opposing valves, × 2 and × 6 respectively; L, specimen from Gulgong illustrated by Mueller (1878, pl. XV, figs 6, 7), × 1.5.

vertical axis. The species thus differs from *E. angularis* which is 3-loculate and radially symmetrical about the vertical axis.

DISTRIBUTION. Gulgong (Home Rule, Black Lead, Forest Reef), NSW (Mueller 1877, 1879; Barnard 1881; herein); Haddon (Nintingbool, ?Crucible Co. Shaft, ~23.2m), Foster, Victoria (Mueller 1883; Deane 1925).

AGE RANGE. Early-Late Miocene.

AFFINITY. In possessing 2 locules, a smooth surface sculpture and a flanged-bilateral shape they are comparable to *E. polyandrus* A.C.Smith, which occurs on the Solomon Islands (Coode, 1978). The smooth stones of extant *E. largiflorens* C.T.White, *E. foveolatus* F.Muell., *E. ferruginifloris* C.T.White, and *E. thelmae* Hyland & Coode differ in being 3-loculate.

Elaeocarpus brachyclinis (F.Muell.) comb. nov. (Fig. 10A-L)

Penteune brachyclinis F.Muell. 1874a: 41, pl. 8, figs 1-9.

MATERIAL. LECTOTYPE (here designated): NMVP6060.(Fig. 10A-D) from the ?Early-Middle Miocene at ~47.5 m in the ?Reform Co. Shaft, at Smythe's Creek, Haddon, Victoria. Two segments of a woody inner mesocarp, originally 5-loculate, near spheroidal; vertical and lateral axes each 17mm. Segments concave externally; internally separated by the central axis, which comprises a cylinder of longitudinally orientated vascular strands extending from the base to near the apex. Locules unequal in size, one with a seed cavity and the other laterally compressed; endocarp with tangentially orientated cells. Mesocarp wall 3mm thick with pitted external sculpture. Endocarp wall thin. Seed cavity ovoid, 14-15mm long, 5-6mm wide; seed near apical, fusoid, incompletely preserved. Seed 10mm long with lateral axes of 6mm and 4mm (Mueller, 1874a, pl. 7, figs. 5,6).

DESCRIPTION. Fruit stones near spheroidal, vertical axis 15-22mm, lateral axes 15-19mm; 5-loculate and with longitudinal sutures delimiting the segments that are externally concave to straight sided; sculpture smooth to pitted. Mesocarp wall 3-4mm thick, adjacent endocarp wall thin, enclosing ovoid seed-containing or compressed locules. Seed ovoid with near apical attachment, bitegmic. Outer epidermis of testa with longitudinally arranged rectangular cells up to 80μm long and 20μm wide; inner epidermis with cuboid, thin walled cells. Outer epidermis of tegmen with elongated dumb bell-shaped lignified cells, with 18-20μm thick, pitted walls.

REMARKS. The original description was based on 'a solitary specimen'; only 2 segments of this

lectotype has been located. It is partially pyritised with adherent mineral matter. Another figured specimen (Mueller, 1874a, pl. 7, figs 7-9) is named *Penteune brachyclinis* F. Muell., but in the discussion is considered to connect *P. clarkei* and *P. brachyclinis*. This specimen, with externally concave segments, has not been located. It remains uncertain whether or not external shape of the segments is definitive for the 2 taxa as Mueller (1874a: pl. 7, fig. 2) depicted a specimen of *P. clarkei* with externally concave segments. Other specimens have externally concave (Fig.10H) or flat (Fig.10 F,G) surfaces.

COMPARISON. Similar to *E. clarkei*, differing in being spheroidal rather than prolate and smaller. Mueller (1874a: 41) considered 'it not improbable that they' (*P. clarkei*, *P. brachyclinis*) 'constitute merely varieties of one species'.

DISTRIBUTION. Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5m and Nintingbool, Crucible Co. Shaft, ~23.2m), Victoria (Mueller 1874a, 1875); Gulgong (Black Lead), NSW (Barnard 1881).

AGE RANGE. ?Early- Middle to Late Miocene.

AFFINITY. Selling (1950) indicated affinity with *Elaeocarpus*. The species resembles fruit stones of extant *E. bancroftii* F.Muell. & Bailey, which, however, are rarely 5-loculate, and are larger and ovoid with segments that have convex external faces.

Elaeocarpus cerebriformis Rozefelds & Christophel, 1996

Elaeocarpus sp. Christophel, 1994, fig. 2.10E.
Elaeocarpus cerebriformis Rozefelds & Christophel 1996b: 232, fig. 2a-h, 4a.

MATERIAL. HOLOTYPE (by original designation) UAY001 from late Early-Late Miocene Yallourn Formation in the Yallourn Coal Mine, Latrobe Valley, Victoria.

DESCRIPTION. Fruits prolate ellipsoidal, vertical axis 10.1-12.2mm, transverse axis 7-8.1mm; 3- or more rarely 2-loculate, with longitudinal sutures delimiting the segments, the outer surfaces of which are sculpted by prominent verrucae and rugulae, the bases of which form arches up to 2.5×5mm in diameter and 1mm high; crests overlie supporting columns and inter-communicating arches. Mesocarp wall 1.1-1.12 mm thick, endocarp of tangentially aligned elongated cells. Fertile locules ellipsoidal, up to 8mm long and 4mm wide. Seed
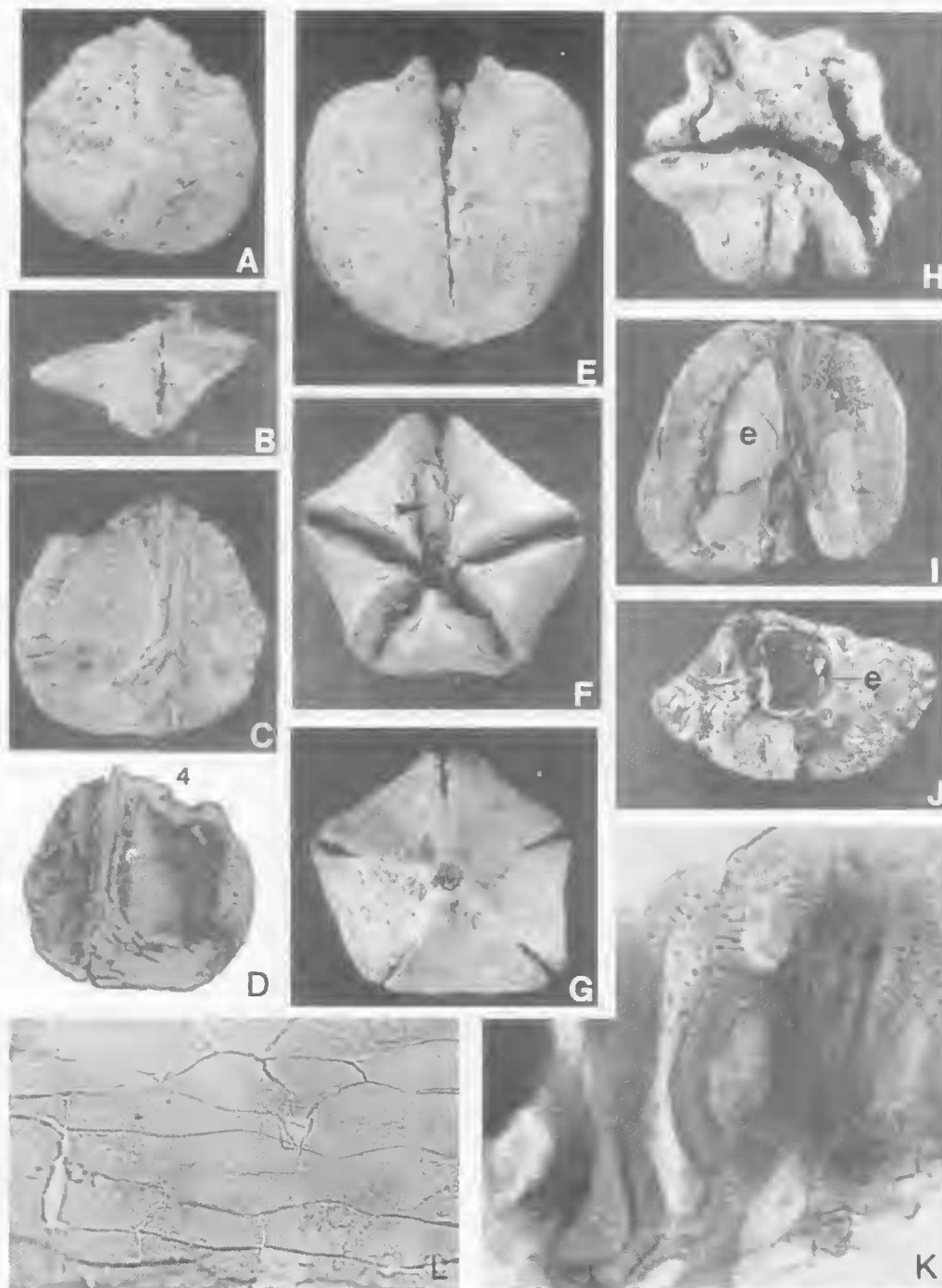
FIG. 10. *Elaeocarpus brachyclinis* (F.Muell.) comb. nov., fruit stones and seeds. A-D, lectotype , NMVP6060, × 2, comprising 2 segments of an originally 5-loculate fruit stone. A, lateral view; B, apical view; C, internal surface; D, Mueller's (1874a, pl. 8, fig. 4) illustration, × 2, of mirror image of specimen. E-G, lateral, apical, and basal views of a specimen containing a seed (arrow), × 2. H, apical view of specimen with concave segments, × 2; I, internal view of 2 segments showing endocarp (e) and seedless compressed locule, × 2. J, transverse section of segment showing endocarp section (e) and seed coat (arrow) in locule, × 2. K-L, seed illustrated in J; K, outer epidermis of tegmen, × 750; L, outer cuticle of testa, × 250.
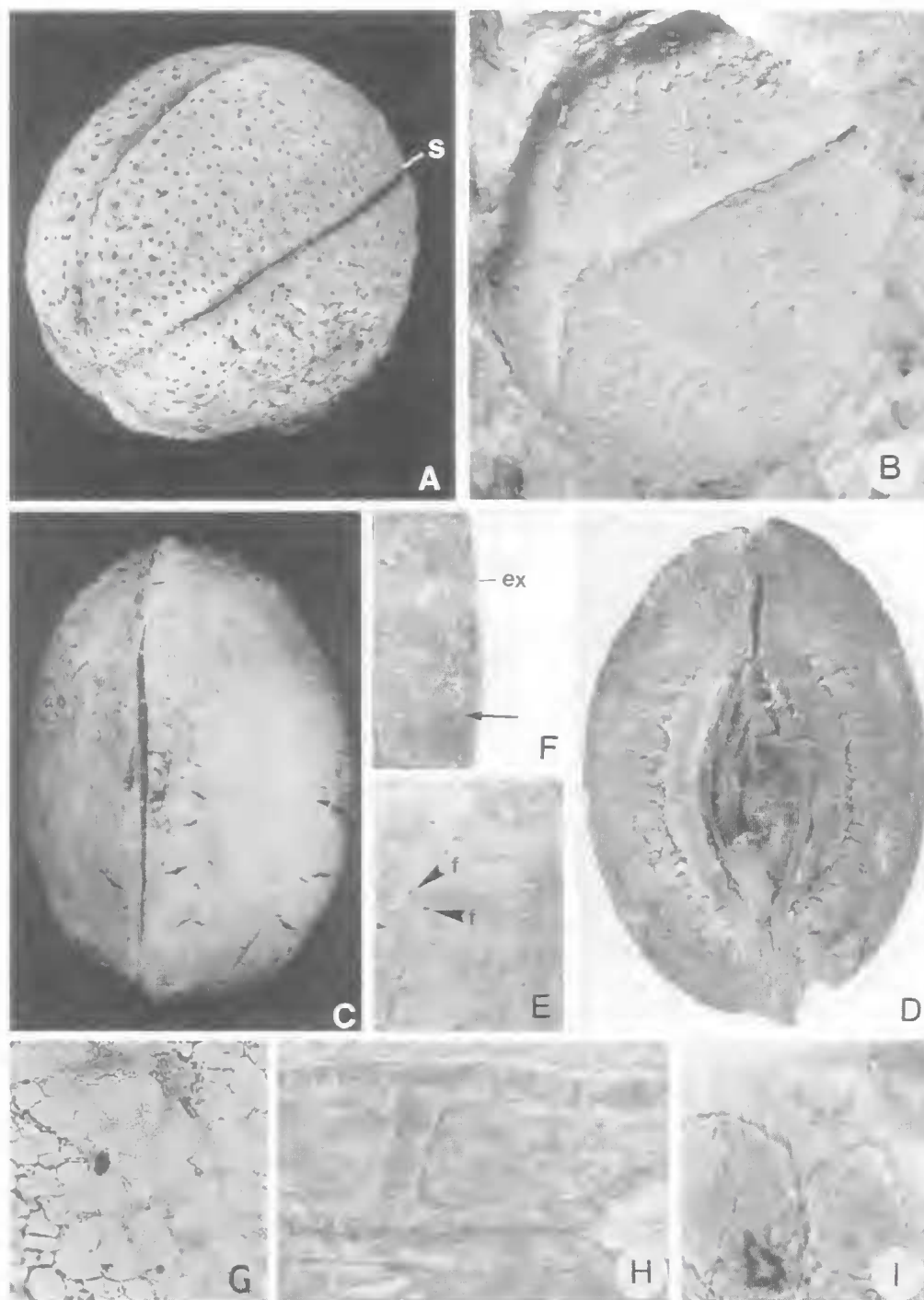
FIG. 11. *Elaeocarpus clarkei* (F.Muell.) Selling, fruit stones and seeds. A, B, oblique lateral view of fruit stone, neotype (AMF9281), × 2; A, showing stalk scar and longitudinal sutures (s) of latex cast; and B, mould. C, D, lateral view of two segments of fruit, × 2, with outer mesocarp and exocarp preserved; C, exterior ; D, interior. E, F, detail of exocarp; E, surface showing fibre ends (f), × 4; F, section showing junction between the outer and inner mesoearp (arrow), × 6. G-I, tegmen; G, detail of cuboid cells, × 250; H, outer epidermis of elongated sclereids with pitted walls, × 500; I, spheroidal sclereids, × 500.

anatropous, ellipsoidal with rounded apex. Anatomy of seed coat unknown.

COMPARISON. The 2-3 segmented fruits are prolate ellipsoidal and differ from *E. mackayi* which is spheroidal. *E. spackmaniorum* has 5 segments and is spheroidal and *E. cunningii* has smaller sculptural elements.

DISTRIBUTION AND RANGE. Yallourn, Victoria in late Early-Late Miocene sediments.

AFFINITY. Similar to *Elaeocarpus* sp. nov. 1 (Coode, 1984)/ *E.* sp. (Mossman Bluff, Henderson, 1997) from N Queensland (Rozefelds & Christophel, 1996b).

Elaeocarpus clarkei (F.Muell.) Selling, 1950 (Fig. 11A-I)

Penteune clarkei F.Muell. 1874a: 41, pl. 7, figs 1-10.
Elaeocarpus clarkei (F.Muell.) Selling 1950: 558.

MATERIAL. NEOTYPE (designated Rozefelds & Christophel, 1996a: 43, pl. 1, figs A-C): AMF9281 (Fig. 10A, B, from Early Miocene at Elsmore, NSW. Mould in ironstone from which latex casts have been made. Vertical axis 31mm, transverse axes 29mm, with 5 longitudinal sutures, with punctate ornament. Internal structure of mesocarp and seeds unknown.

DESCRIPTION. Fruits with 5 or rarely 4 locules, prolate ellipsoidal; vertical axis 25-41mm long; each transverse axis 19-34mm; apex and base rounded or slightly pointed. Mesocarp segments delimited by longitudinal sutures, with convex to slightly concave outer surfaces; inner woody mesocarp with punctate sculpture, sometimes overlain by the thin, fibrous outer mesocarp and exocarp. Fruit segments separated internally by the central axis that comprises longitudinally orientated vascular strands. Inner mesocarp wall 4-6mm thick, compact. Locules enclosed by thin endocarp; with a seed cavity or compressed. Seed cavity fusiform, up to 16mm long and 10m wide. Testa with outer epidermis composed of isodiametric cells. Tegmen multiplicative; outer epidermis comprising fibriform, lignified cells up to 200µm long, with pitted walls 20µm thick. Underlying cell layers of lignified cuboid cells and parenchyma.

REMARKS. Mueller (1874a) based the species on charcoalified specimens from Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5), Vic., but this material was presumed lost or destroyed by Rozefelds & Christophel (1996a) who selected a neotype from Elsmore, NSW and redefined the species. The Museum of Victoria collection contains specimens from Haddon

(Smythe's Creek, ?Reform Co. Shaft, ~47.5m) which have a thick mesocarp wall and internally abut a cylinder of vascular strands that extend from the base to ~ midway to the apex. Comparable features are displayed by a specimen illustrated from Victory Mine, Orange (Fig.11C,D).

COMPARISON. *Elaeocarpus clarkei* (F.Muell.) Selling) is similar to, and may be conspecific with, *E. allportii*. *E. brachyclinis* is similar, but is smaller and spheroidal.

DISTRIBUTION. Elsmore, Bathurst, Carcoar-Orange, Orange (Forest Reefs, Victory Mine) and Gulgong (Black Lead), NSW (Mueller, 1876, 1883; Barnard, 1881; Rozefelds & Christophel, 1966a); Boola Boola. Foster (deep leads), Beechworth (Eldorado), Talbot (Victory Mine, Homebush Lead) and Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5m), Vic. (Mueller, 1874a, 1874b, 1883; Deane, 1925; Rozefelds & Christophel, 1996a); Beaconsfield (Brandy Creek), Tasmania (Johnston, 1880a).

AGE RANGE. Oligocene-Miocene.

AFFINITY. Selling (1950) first identified the species with *Elaeocarpus*. The species is similar in size, shape and sculpture to fruits of *E bancroftii* F.Muell. & Bail. and *E. linsmithii* Guymer, but differs in that the locule number in *E. bancroftii* is usually 4, and rarely 3 or 5, while *E. linsmithii* has 2 locules (Guymer, 1984).

Elaeocarpus couchmanii (F.Muell.) comb. nov. (Fig. 12A-G)

Pleioclinis couchmanii F.Muell. 1882: 43, pl. 19, figs 1-11.

MATERIAL. LECTOTYPE (here designated): NMVP53920 (Fig. 12A-D). Location uncertain: either from the ?Early -Middle Miocene at ~23.2m in the Crucible Shaft or ~47.5m in the Reefton Shaft at Smythe's Creek, Victoria. Six segments of 8-loculate specimen. Mesocarp woody, originally 8-loculate, and near-spheroidal (vertical axis 21.5mm, transverse axes 20.5mm). Segments with external fossulate sculpture, delimited by longitudinal sutures extending from base to apex, and internally abut central hollow cylinder of vascular strands; wall 3-3.5m thick at segment junctions. Locules developed unequally, 2 originally with a seed cavity; others compressed; endocarp wall thin. Seed cavity ellipsoidal, vertical axis 19mm, lateral axis 8mm; seed with near apical attachment, oblique ellipsoidal, 15mm long, 5mm wide.

DESCRIPTION. Fruit stones woody, near-spheroidal, 12-25mm max. diameter, usually with 8, less frequently with 6-9 locules seed bearing or compressed within thin-walled endocarps, which are enveloped by the inner mesocarp. Mesocarp segments delimited by
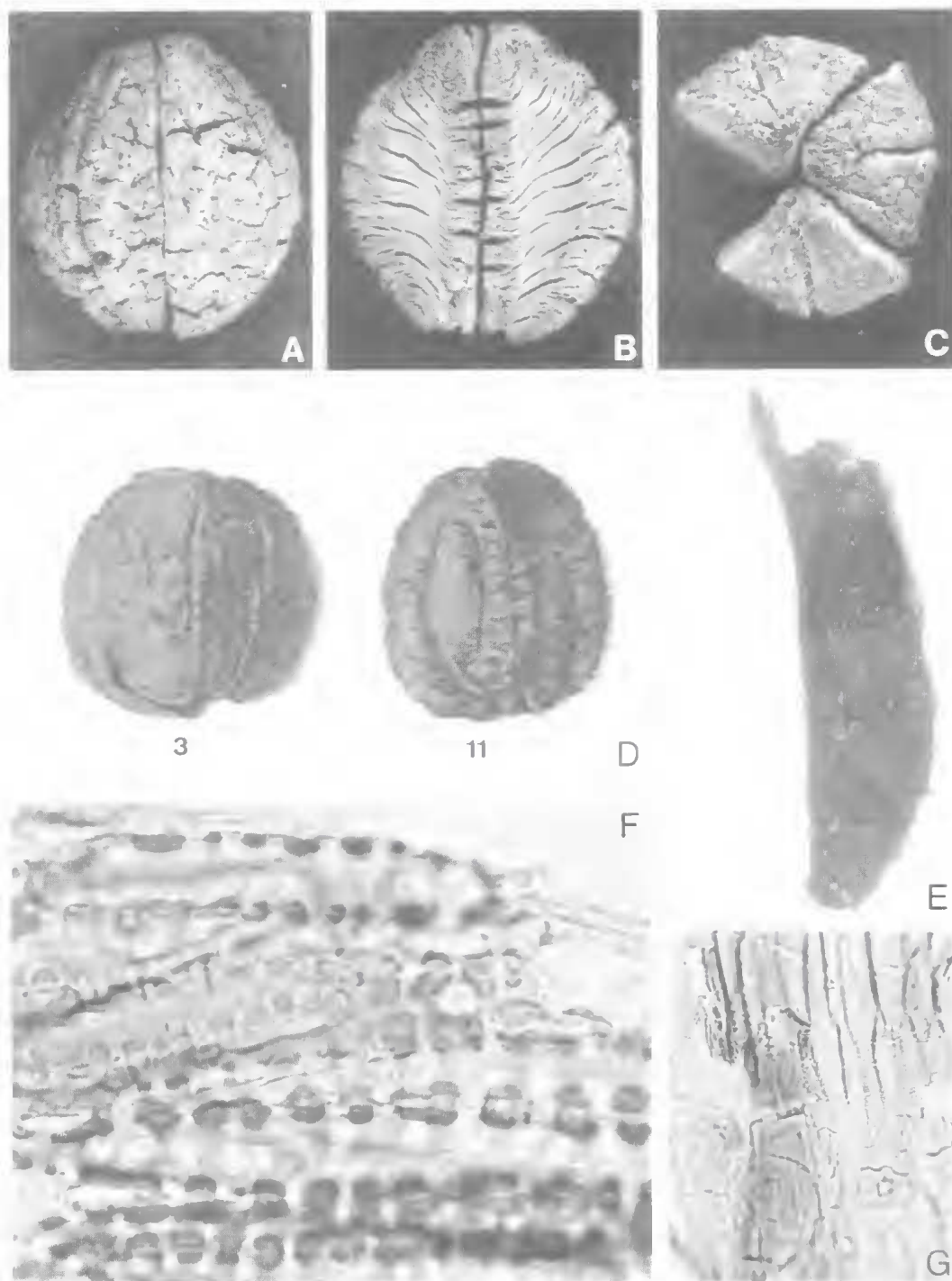
FIG. 12. *Elaeocarpus couchmanii* (F.Muell.) comb. nov., fruit stone and seeds. A-C, lectotype (NMVP53920), ×
2, comprising six segments of original 8-segmented fruit stone. A, lateral view; B, internal view of two fused
segments; C, apical view. D, Mueller's (1882, pl. XIX, figs 3, 11) illustrations of lectotype, × 1.5, but note
image in his fig. 11 is reversed and seed illustrated in left hand locule has not been located. E-G, seed; E, whole
specimen showing lenticular shape and apical funicle, × 10; F, outer epidermis of tegmen showing
thick-walled, pitted elongate sclereids, × 750; G, outer cuticle of testa, × 250.
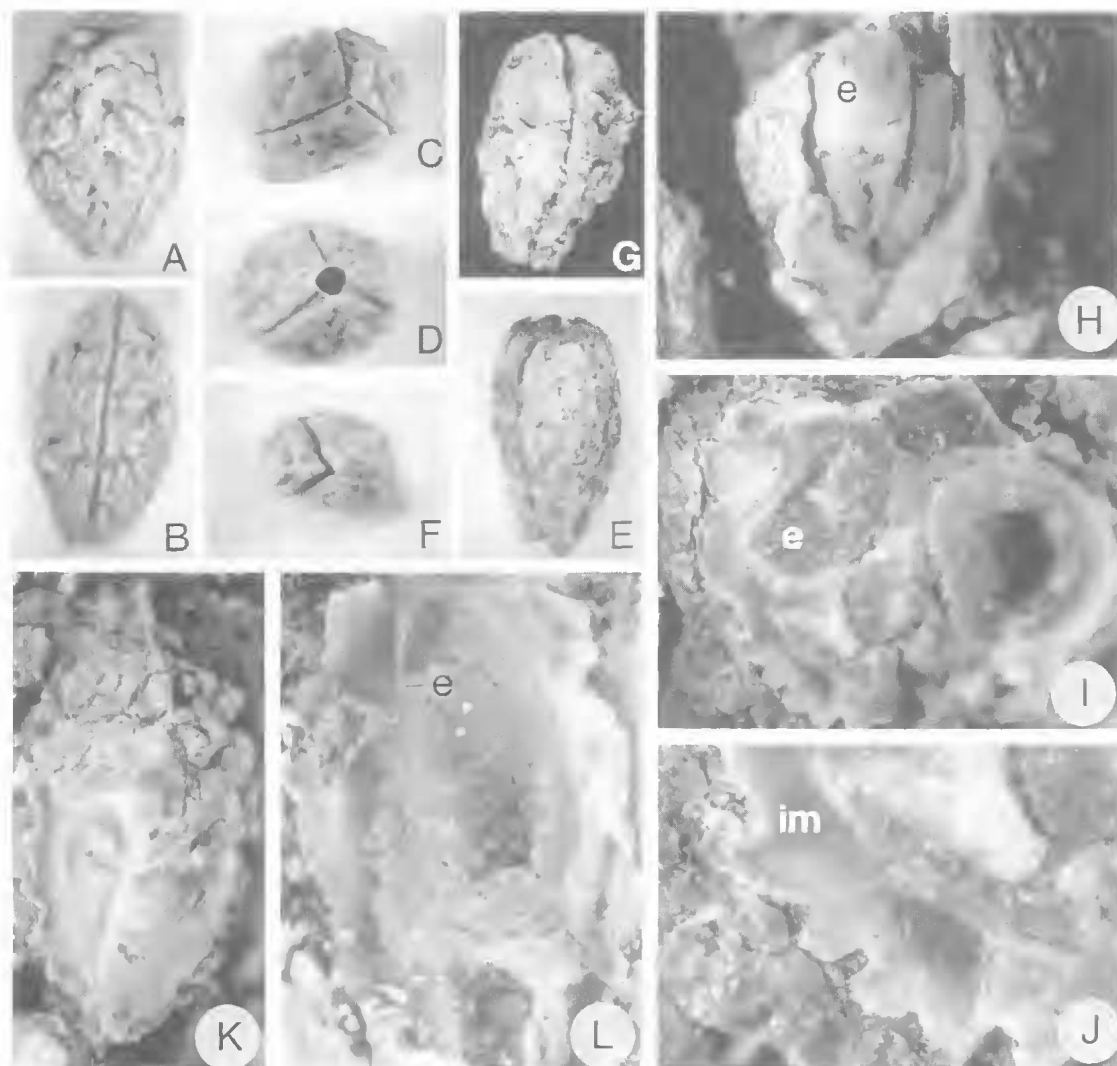
FIG. 13. *Elaeocarpus cunningii* Rozefelds, fruit stones. A-D, permineralised holotype (QMF16768, see Rozefelds, 1990, fig. 6D, right hand specimen), × 3. A, B, lateral views; C, apical view; D, basal view. E-G, charcoalified specimen, × 3; E, G, lateral view; and F, apical view. H, permineralised specimen in lateral view with partially exfoliated inner mesocarp showing endocarp (e) surrounding locule (see Rozefelds, 1990, fig. 6E, top left specimen), × 6. I, J, transverse section of 3-loculate permineralised specimen showing sculptured inner mesocarp (im), endocarp (e), and two fully developed locules, the third compressed, × 10, × 25 respectively. K, permineralised specimen, oblique longitudinal section showing two locules, endocarp wall, and surface and sectional views of sculptured inner mesocarp, × 6. L, longitudinal section of permineralised specimen showing crystal infilled locule, endocarp wall (e) and ~tangential section of inner mesocarp, × 10.

longitudinal sutures, with external fossulate sculpture; wall 3-4mm thick, of compact isodiametric cells with lignified walls. Endocarp with tangentially orientated elongate cells. Seed cavity ellipsoidal to fusiform; seed with near apical attachment, oblique ellipsoidal. Testa with an outer cuticle of rectangular cells; outer epidermis of tegmen of lignified, fibriform cells (up to 150μm long, 2μm wide) with thick (4-6μm), pitted walls. Underlying cell layers include tannin infilled cells (up to 50 × 100μm).

REMARKS. Mueller's other syntypes were not found, but material collected shortly thereafter from Nintingbool and Gulgong (Black Lead) has been examined.

COMPARISON. *E. couchmanii* differs from the 8-loculate *E. pleioclinis* in being larger and having a spheroidal, not prolate ellipsoidal, shape. Moreover, the segments of *E. pleioclinis* are externally concave and near smooth.

DISTRIBUTION. Haddon (Nintingbool, Smythe's Creek), Victoria; Gulgong (Black Lead), NSW (Mueller, 1882); Bethany, South Australia (Hossfeld, 1949).

AGE RANGE. Early–Late Miocene.

AFFINITY. Eight-loculate fruit stones with fossulate sculpture are not represented among Australian extant *Elaeocarpus*.

Elaeocarpus cunningii Rozefelds, 1990
(Fig. 13A-L)

MATERIAL. HOLOTYPE (by original designation): QMF16768 from the ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Mesocarp prolate ellipsoidal, vertical axis 10mm long, lateral axes each 6.5mm; 3-loculate and with 3 longitudinal, equally spaced sutures. Surface sculpted with verrucae and rugulae that have rounded crests and irregularly elongated bases up to 3mm in length.

DESCRIPTION. Mesocarp 3-4-loculate, prolate ellipsoidal, vertical axis 7-14mm, lateral axes 4.6-8.3mm. Surface sculpture verrucate-rugulate; elements with irregularly elongate bases up to 1 × 3mm, with rounded crests projecting up to 2mm from surface. Longitudinal sutures delimit 3 or rarely 4 segments. Locules unequal; 2 are with a seed cavity, the other compressed. Mesocarp wall up to 1mm thick, endocarp wall < 0.1 mm thick; mesocarp and seed anatomy unknown.

REMARKS. The description is based on permineralised specimens from the type locality and a compressed charcoalified specimen from Picardy Station, Moranbah.

COMPARISON. *Elaeocarpus cunningii* and *E. cerebriformis* Rozefelds & Christophel are similar in size, shape, and in possessing 3 locules, but sculpture of the latter species comprises considerably larger verrucae and rugulae.

DISTRIBUTION. Glencoe near Capella, Moranbah (Picardy RDPD98MA17, 111-133m), Queensland.

AGE RANGE. Early Oligocene-?Miocene.

AFFINITY. Rozefelds & Christophel (1996b, table 2) compared the sculpture of *E. cunningii* with that of extant species including *E. reticulatus* Smith. However, the extant species has both echinae and verrucae (Fig. 7A-D). Fruit

stones of *E. holopetalus* F.Muell. have similar sculpture but are usually 2-loculate.

Elaeocarpus johnstonii
(F.Muell.) comb. nov.

Rhytidotheca johnstonii F.Muell. in Johnston 1882: 50, fig. 60-a.
Elaeocarpus bassii Ettingshausen 1883: 63, pl. 6, figs 9-12.

MATERIAL. HOLOTYPE: Specimen (Mueller in Johnston, 1882, fig. 60-a) from the Oligocene at Beaconsfield (Brandy Creek), Tasmania. This description is based on that given by Ettingshausen (1888) and the illustrations provided by him and by Johnston (1882). Mesocarp perprolate, ellipsoidal, with acute base and apex, length 26mm, axes of lateral section 7 × 13mm; 5- loculate and with 5 equal segments, each delimited externally by a suture that extends from the base to the apex. Surface with medium-high relief sculpture of irregular verrucae. Internal features not known. LECTOTYPE (here designated) of *E bassii*: Ettingshausen 1883, pl. 6, figs 11, 12 from the Oligocene at Beaconsfield, Tasmania.

REMARKS. Mueller's (Johnston, 1882, fig. 60-a) and Ettingshausen's (1883, pl.6, figs 11, 12) specimens from the 'Johnston collection' could not be located. The similarity of the illustrations and the remarks of Etheridge (in Ettingshausen, 1888: 63, footnote) indicate that *E. johnstonii* and *E. bassii* are based on the same specimen; accordingly the former is a senior synonym of the latter.

COMPARISON. *E. johnstoni* has 5 locules and resembles 5-locular specimens of *E. lynchii* in size and shape, but differs in having more prominent sculpture.

DISTRIBUTION. Beaconsfield (Brandy Creek), Tasmania; Ettingshausen's (1883, table II) reference to the 'Derwent District, Tasmania' is not supported by any specimen or illustration and so may be incorrect.

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. With *Elaeocarpus* as suggested by Ettingshausen (1883) who made comparison with *E. angustifolius*, which, however, are spheroidal (Fig. 5).

Elaeocarpus lynchii (F.Muell.)
Selling, 1950
(Fig. 14 A-O)

Rhytidotheca lynchii F.Muell. 1871b: 39, pl. IV, figs 1-8.
Elaeocarpus lynchii (F.Muell.) Selling 1950: 559.

MATERIAL. LECTOTYPE (here designated): NMVP6033, NMVP6034. (Fig. 12A-H) from the ?Early-Middle Miocene at ~25.2m in the Crucible Shaft, Nintingbool, Haddon, Victoria. Two segments of a
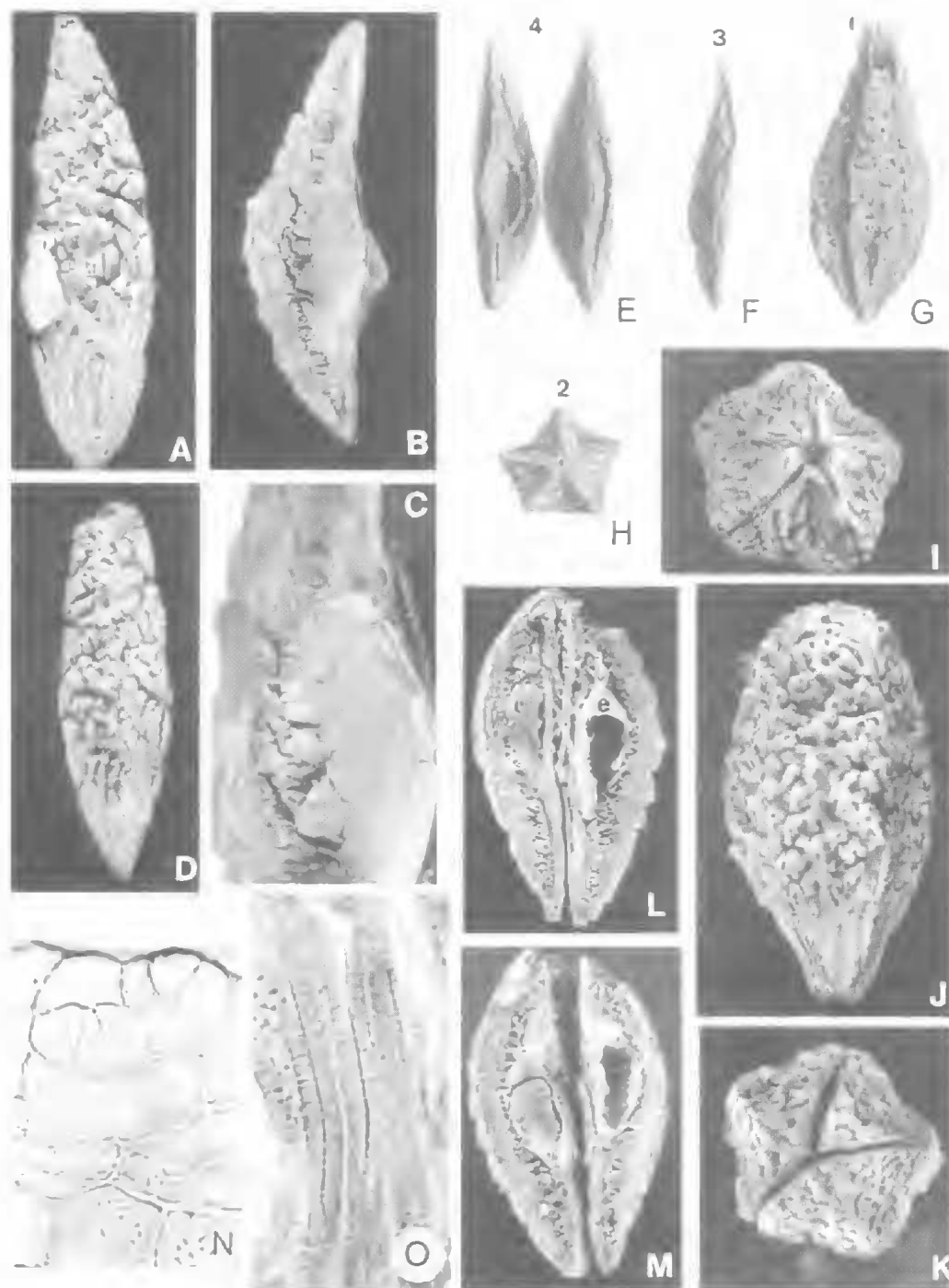
FIG. 14. *Elaeocarpus lynchii* (F.Muell.) Selling, fruit stones and seeds. A-D, lectotype comprising two segments of original 5-segmented fruit stone. A, external; and B, C, internal surfaces of one segment (NMVP6034); A,B × 2, C, × 4. D, external surface of other segment that is broken at apex (NMVP6035), × 2. E-H, Mueller's (1871c, pl. IV, figs 1-4) illustrations of lectotype, × 1.2. I-K, basal, lateral, and apical views respectively of well preserved fruit stone, × 2. L, M, internal views of 4-loculate specimen showing endocarps (e) and seed cavities, × 2. N-O, outer cuticle of testa showing N, hair bases and isodiametric cells, × 250; and O, sclereids with thick, pitted walls from outer epidermis of tegmen, × 500.

dehisced 5-locular specimen (Mueller 1871b, pl. 4, figs 1-4). NMVP6033, representing centre segment in Mueller's fig. 1. Segment broken near distal end, with an acute base and broadening to 8mm midway between base and apex, 28 mm long; exposed locules seedless, compressed. Mesocarp wall 3.8 mm thick, with external sculpture of low (<1mm high), narrow (up to 1mm wide) sinuous rugulae and verrucae. NMVP6034, left hand segment in Mueller's fig. 4. Segment acute at base and apex, broadening to 9mm; length 34.5 mm; sculptured externally with sinuous rugulae and verrucae (<1mm high, 1mm wide). One locule with a seed cavity, the other compressed; endocarp wall thin (<0.2 mm thick), of elongated tangentially aligned cells; mesocarp wall 3.5mm thick. Seed cavity acutely ellipsoidal, longitudinal axis 10mm, transverse axis 4.5mm. Seed presumed lost or destroyed.

DESCRIPTION. Fruit stones perprolate, fusiform with an acute base and acute to rounded apex, length 28-36mm, axis of lateral section 10-17mm; 5-loculate and with 5 segments, each delimited by a longitudinal suture extending from base to apex; dehiscence loculicidal. Surface with low relief sculpture of narrow sinuous rugulae and verrucae but near smooth in abraded specimens. Locules with a seed cavity situated midway between the base and apex or compressed; seed cavity more than twice as long as wide; endocarp composed of tangentially aligned elongated cells. Seeds with near apical attachment, fusiform. Testa with outer cuticle of rectangular and polygonal cells up to 60-80μm in diameter interspersed with groups of 2-3 smaller subcircular cells representing hair bases. Tegmen with outer epidermis of fibriform, elongated sclereids (up to 120μm long, 10μm wide) with thick (5-6μm) pitted walls. Underlying layers include sheets of isodiametric parenchyma cells, some of which are tannin infilled.

COMPARISON. *Elaeocarpus lynchii* is readily distinguished from other fossil mesocarp taxa referable to *Elaeocarpus* by its perprolate shape in combination with the low relief rugulate sculptural pattern. *E. johnstonii* has a similar shape and locule number, but differs in its high relief sculpture.

DISTRIBUTION. Haddon (Ningtinbool, ?Crucible Co. Shaft, ~25.2m), Smythsdale, Foster, Victoria (Mueller, 1871b; Deane, 1925); Gulgong (Black Lead 44.5m), NSW (Barnard, 1881); Bethany, South Australia (Hossfeld, 1949).

AGE RANGE. Early-Late Miocene.

AFFINITY. Inclusion in *Elaeocarpus* was proposed by Selling (1950) which is fully supported by features of the fruit stones, seed attachment, and seed coat. Fruit stones of extant *E. grahamii* F.Muell. are similar in shape and sculpture, but are 2-loculate.

Elaeocarpus mackayi (F.Muell.) Kirchheimer, 1935
(Fig. 15A-I)

Phymatocaryon mackayi F.Muell. 1871a: 47, pl. 2, figs 1-15. *Elaeocarpus mackayi* (F.Muell.) Kirchheimer 1935: 180.

MATERIAL. LECTOTYPE (designated here) NMVP53562 (Fig. 15A, B) from ?Early-Middle Miocene at ~47.5m in Reform Co. Shaft at Smythe's Creek, Haddon, Victoria. Mesocarp subspheroidal, vertical axis 22mm, transverse axes each 24mm; with prominent sculpture of verrucae and rugulae up to 2 x 6mm in basal diameter and 1-2mm high. Mesocarp overlain in places by remains of externally smooth exocarp and outer mesocarp, which is 2mm thick; 3-loculate, with 3 external longitudinal sutures. Inner mesocarp wall 4mm thick, compact; locule wall composed of tangentially orientated elongated cells. Two locules with seed cavity, the other compressed. Seed cavity ovoid, 12mm long, 10mm wide. Seed coat bitegmic. Testa with outer cuticle of isodiametric cells 60-70μm in diameter; outer epidermis of tegmen with a lattice of elongated sclereids with thick (5-6μm), pitted, lignified walls.

DESCRIPTION. Fruit stones spheroidal to prolate-ellipsoidal with conspicuous external verrucate-baculate sculpture interrupted by 2 or more usually 3 evenly spaced longitudinal grooves. Broken specimens reveal 3 or rarely 2 locules of which 1 or 2 contain a single near apical, axial seed and the other locule(s) are sterile and compressed. Woody inner mesocarp wall 4-5mm thick, of compact isodiametric cells; endocarp of tangentially orientated elongated cells. Vertical axis of mesocarp a cylinder of strands extending from base to near the apex. External surface of mesocarp sculpted with anastomising verrucae, bacula, and rugulae that have irregular bases up to 2 6mm in diameter and which are separated by narrow grooves up to 1mm wide and 1-2mm deep. Seed ovate (up to 10mm long, 6mm wide), attachment near apical; seed coat bitegmic.

REMARKS. The species is based on coalified specimens, 2 (including the lectotype) of which show traces of a fleshy outer mesocarp (sarcocarp of Mueller, 1871a: 47). Material examined includes the types and other specimens from the type locality, collections from Gulgong (MMF), and compressed specimens from Picardy Station, Moranbah and from near Blackwater. The Queensland specimens range
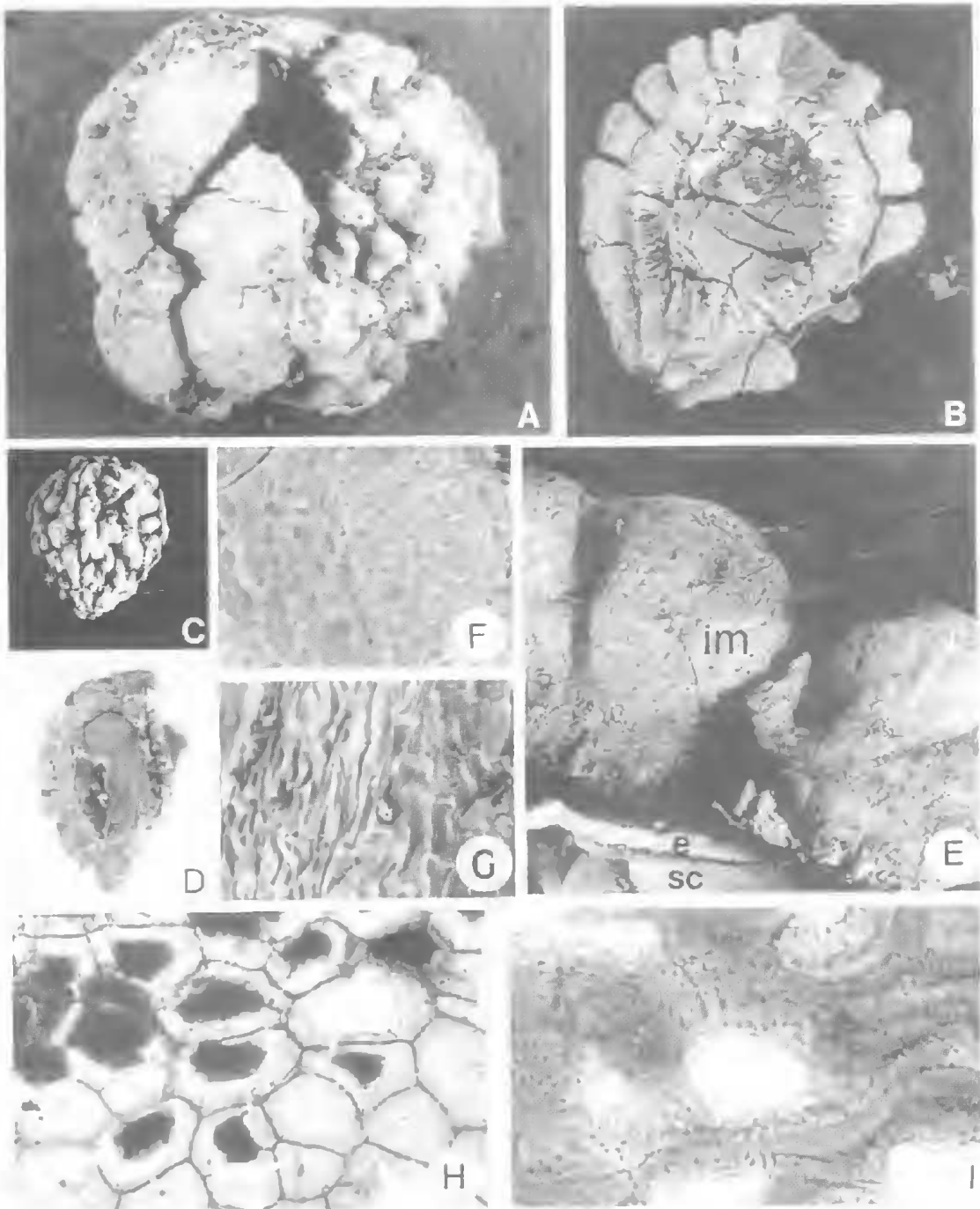
FIG. 15. *Elaeocarpus mackayi* (F.Muell.) Kirchheimer. fruits and seeds. A, B, lectotype (NMVP53562. see Mueller, 1871b, pl. ll, fig. 4; Rozefelds & Christophel, in press. fig. 2A, B). A, lateral view showing preserved outer mesocarp overlying sculptured inner mesocarp; B, inner surface of segment showing seed cavity, × 2. C, lateral view of small specimen, × 2. D, inner surface of specimen with seed locule showing endocarp (e) and enclosed seed, × 2. E, section of inner mesocarp (im), endocarp (e) and seed coat (sc), × 30. F, cell structure of inner mesocarp, × 200. G, inner surface of endocarp wall of compressed locule, × 300. H, outer cuticle of testa, × 250. l, sclereids with thick, pitted walls from outer epidermis of tegmen of lectotype, × 500.

6.25 (8.1) 10.2mm long and with transverse axes 5.52 (7.4) 9.3mm and 3.8 (4.8) 9.1mm, and approximate the size of the smaller specimens of Mueller (1871a, pl. 2, figs 8, 9, 13-15).

COMPARISON. *E. mackayii* and *E. spackmaniorum* are similar in their sculptural attributes and 3-loculate specimens of the latter may imply intergradation of the species. *E. mackayii* differs from *E. cerebriformis* in having a near spheroidal shape. *E. cunningii* is prolate-ellipsoidal and has sculpture of smaller-based and lower elements.

DISTRIBUTION. Haddon (Symthe's Creek, Reform Co. Shaft, ~47.5m), Beechworth (Eldorado), Tanjil, Victoria (Mueller, 1871a, 1874b; Deane, 1925); Dubbo, Orange (Victory Mine, Forest Reefs), Gulgong (Black Lead 146 ft.), NSW (Mueller, 1874b, Barnard, 1881, Rozefelds & Christophel, in press); Launceston, Tasmania (Mueller, 1883); Bethany, South Australia (Hossfeld, 1949). Recorded herein from near Moranbah (Picardy RDPD98MA17, 111-133m, Picardy RDPD98MA21, 123-133m) and South Blackwater (Hole R8736, 82m).

AGE RANGE. Early Oligocene-Miocene.

AFFINITY. With *Elaeocarpus* as recognised by Deane (1925), Kirchheimer (1935), Selling (1950) and Rozefelds & Christophel, who note congruence with fruit stones of *E. angustifolius*, but these differ in being 5- or rarely 4-loculate.

Elaeocarpus muelleri Ettingsh., 1886

Elaeocarpus muelleri Ettingsh. 1886: 157, pl. 14, figs 4, 5.

MATERIAL. LECTOTYPE (here designated): Ettingsh. 1886, pl. 14, fig. 4: specimen lost according to records of the Australian Museum; from Early Miocene at Newstead near Elsmore, NSW. The description follows that of Ettingshausen. Mesocarp preserved in ironstone, prolate, 5-loculate; external surface with 5 longitudinal sutures and a sculpture of wrinkles.

REMARKS. The species was based on a mesocarp and a leaf from a different locality and horizon; is here restricted to the mesocarp.

COMPARISON. Ettingshausen (1886) indicated that fruit stones of *E. muelleri* differ from those of his *E. bassii*, which is perprolate and has less prominent sutures.

DISTRIBUTION AND AGE RANGE. Type locality; Early Miocene.

AFFINITY. Ettingshausen (1886) suggested close similarity to fruit stones of *E. angustifolius* Blume.

Elaeocarpus peterii Rozefelds & Christophel, 1996
(Fig. 16A-D)

Elaeocarpus peterii Rozefelds & Christophel 1996a: 45, pl. 3, figs A,C,E,G,I.

MATERIAL. HOLOTYPE (by monotypy) QMF18088 (Fig. 16A-D) from ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Mesocarp, oblate ellipsoidal with a broad base, rounded apex, and 6 longitudinal ridges separated by concave surfaces that extend from base to apex; vertical axis 23mm, transverse section stellate, transverse axes each 27mm. Stalk scar circular, 4mm in diameter. Sutures are embedded in the longitudinal ridges. Preserved mesocarp wall 3-5mm in section comprising a thick outer layer and a thin (<1mm) inner layer (?endocarp). Trace of latter layer indicating 2 compressed locules adjacent to central cavity (?fertile locule). External surface with small pits.

REMARKS. The species externally resembles fruit stones of extant *E. stellaris* and undescribed *Elaeocarpus* sp. from N Queensland (Rozefelds, pers comm.) in shape and longitudinal sutures embedded in the projecting ridges. The hollow central region implied to Rozefelds & Christophel (1996a: 45) that 'replacement of internal mesocarp structure has not occurred'. This central region is partially infilled and surrounded by a layered wall, the outer broad layer of which may represent the mesocarp and the narrow inner layer the endocarp. Moreover, the trace of the endocarp implies 2 compressed locules adjacent to the main central cavity, which may represent the seed cavity. The banding represented in the inner mesocarp (Fig. 16C) is due to layering in the opaline silica and is unrelated to original structures.

COMPARISON. External morphology resembles that of the charcoalified specimens assigned to *E. rozefeldsii* sp. nov., and should it be shown that internal organisation of the two taxa be comparable, the latter species will be a junior synonym of *E. peterii*.

DISTRIBUTION AND AGE RANGE. Known only from the type locality in ?Late Oligocene-Early Miocene sediments.

AFFINITY. Rozefelds & Christophel (1996a) considered *E. peterii* similar to fruit stones of extant *E. stellaris*.

Elaeocarpus pleioclinis (F.Muell.) comb. nov.
(Fig. 17A-M)

Rhytidotheca pleioclinis F.Muell. 1873: 42, pl. 6, figs.1-4.
Pleioclinis shepherdi F.Muell. 1882: 43.

MATERIAL. LECTOTYPE (here designated): NMVP53747 two complete segments as originally illustrated (Mueller, 1873: pl. 6, fig. 3,4) and one broken segment of a 8-locular mesocarp (Fig. 17A-D) from ?Early-Middle Miocene at ~23.2m in Crucible Co Shaft,
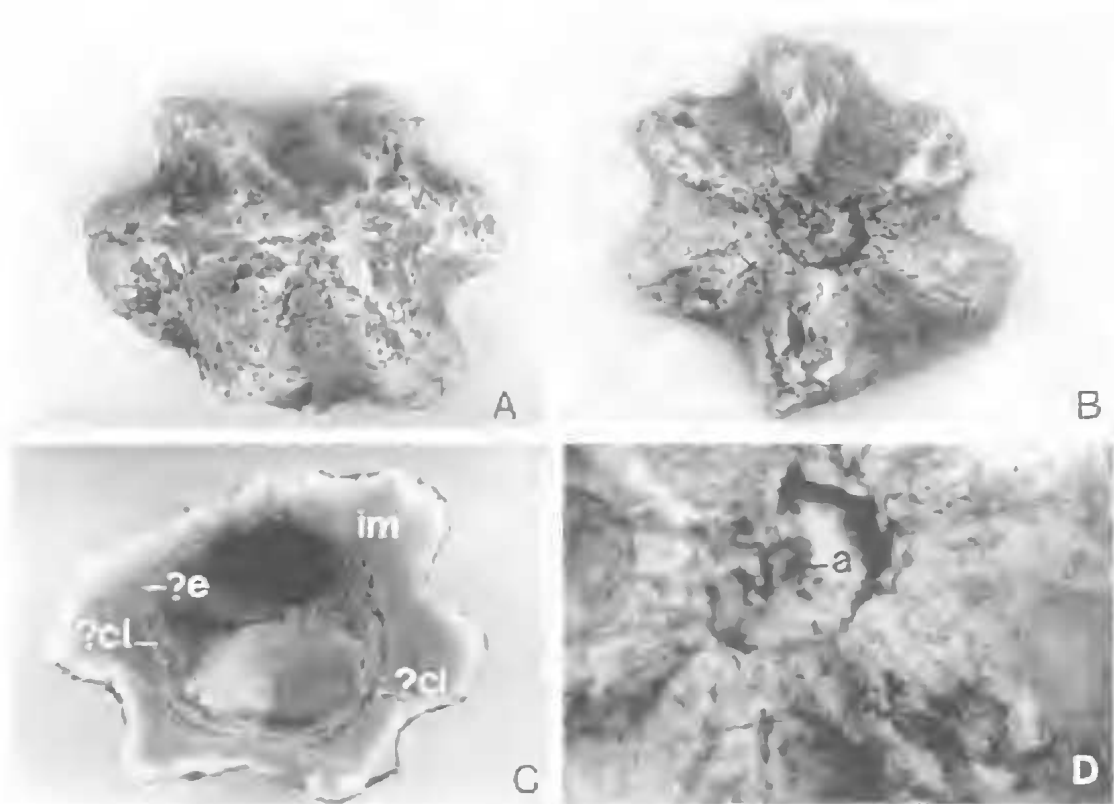
FIG. 16. *Elaeocarpus peterii* Rozefelds & Christophel fruit stone. A-C, permineralised fruit stone, holotype (QMF18088, see Rozefelds & Christophel, 1996a, pl. 3, figs A,C,E,G,I), × 2. A, apical view; B, basal view; and C, transverse section, showing broad banded inner mesocarp (im) probable thin endocarp (?e) and possible compressed locules (?cl). D, detail of base showing vascular tissue in axial canal (a), × 4.

Nintingbool, Haddon, Victoria. Segments 16mm long, with a concave, unsculptured outer surface 5mm wide; internally each segment of 2 half locules one of which has a seed cavity and the other compressed. Mesocarp wall 3mm thick, composed of compact isodiametric cells, but with secondarily radial fractures; endocarp <1mm thick, composed of tangentially aligned cells. Seed cavities up to 10mm long × 2mm wide; seeds not observed.

DESCRIPTION. Fruit stones prolate ellipsoidal, swelling from an acute base to a broadly rounded apex, length 8.1-13.5mm, transverse axes each 6-9mm; 8-loculate and with 8 externally concave segments, each delimited by a longitudinal suture that extends from base to apex. Surface near smooth or irregularly pitted in abraded specimens; mesocarp wall up to 3mm thick, composed of compact isodiametric cells. Locules enclosed by endocarps abut central axis of a cylinder of vertically aligned vascular strands. Endocarp of tangentially orientated elongated cells. Fertile locules with a seed cavity, others compressed. Seed cavity and near apical seed fusiform, at least

twice as long as wide; seed coat bitegmic. Testa with outer cuticle of rectangular cells up to 50μm long and 20μm wide; outer epidermis of tegmen of linearly arranged longitudinal sclereids having thick (4μm) pitted walls overlying a layer of subspherical (40-50μm in diameter) sclerids with similarly thick, pitted walls. Other tegmen tissue parenchymatous layers of thin walled isodiametric cells (up to 20 μm in diameter).

REMARKS. Mueller (1873) based the species on charcoalified specimens, and noted that it comprised a smaller and a larger form. The lectotype is larger than, but otherwise comparable to, the other specimen (Mueller, 1873, pl. 6, figs 1,2) and some other specimens (NMVP53741). In allocating the species to *Rhyditotheca* Mueller (1873: 42) noted that it may 'require generic separation' and later (Mueller, 1882: 43) moved it to *Pleioclinis* introducing the replacement *P. shepherdi* which becomes an objective synonym.
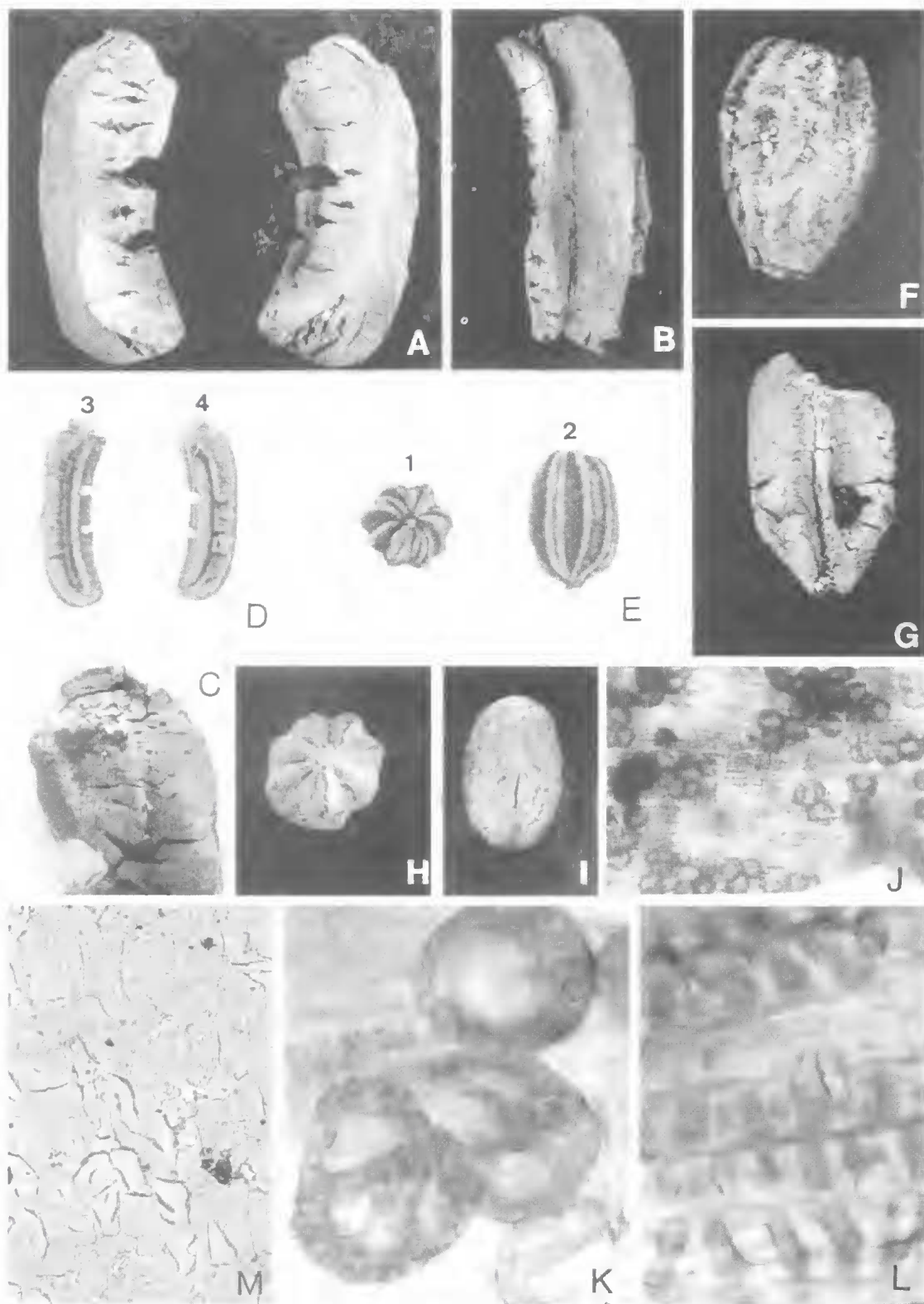
COMPARISON. *E. pleioclinis* possesses 8-loculate fruits, a condition thus far only known among fossil *Elaeocarpus* in *E. couchmanii*. The latter species differs in its larger size, spheroidal shape, and fossulate sculpture.

DISTRIBUTION. Known only from the type locality.

AFFINITY. The organisation of the fruit stone and anatomy of the seed coat are consistent with *Elaeocarpus*. However, extant Australian and New Zealand species with smooth or near smooth sculpture are 3-loculate.

Elaeocarpus rozefeldsii sp. nov.
(Fig. 18A-F)

ETYMOLOGY. For Andrew Rozefelds in appreciation of his helpful discussions and for providing literature.

MATERIAL. HOLOTYPE: QMF50123 (Fig. 18A,C) from Early-Late Oligocene at 82m in South Blackwater Coal Pty Ltd Hole R8736, Near Blackwater, Queensland. Longitudinally ribbed, 7-loculate inner mesocarp, ellipsoidal; compressed obliquely to the vertical plane with vertical axis 18mm, stellate in lateral section, with axes of 18mm and 13mm; base and apex broadly rounded. Seven longitudinal ridges embedded with sutures extend from near base to apex, delimiting segments with externally concave, near smooth faces. Preserved mesocarp wall 2-3mm thick.

DESCRIPTION (7 specimens). Fruit stones woody, 5-7-loculate, ellipsoidal, laterally compressed, stellate in lateral view; vertical axis 14 (16.6) 18mm, lateral section with axes of 14 (16.5) 18mm and 9 (11.8) 13.5mm. Base and apex broadly rounded, the base with a near circular cavity; longitudinal ridges with sutures embedded in their crests extend from base to apex and delimit mesocarp segments that are externally concave and without sculpture. One or more of the locules with a seed cavity, the others compressed; seed cavity up to 6mm long and 5mm wide. Inner mesocarp wall 2-3.5mm thick, anatomy not determined; endocarp <0.5mm thick; internally locules abut hollow axis. Seed cavity ovoid, acute apically, broadening to base, 9-10µm long, 4-5µm wide. Seed fragmented, anatomy of seed coat not determined.

REMARKS. Charcoalified specimens (QMF50-123-50126, QMF51079-51081) included within the species are laterally compressed and have been subjected to abrasion and thermal alteration. Nevertheless their characters (5-7 locules, one or more of which has a seed cavity, loculicidal dehiscence and externally concave segments) support assignment to *Elaeocarpus*.

COMPARISON. *E. rozefeldsii* may be synonymous with *E. peterii* should the latter species be shown to possess 5-7 locules. In possessing externally concave, near-smooth segments, *E. rozefeldsii* is similar to *E. pleioclinis*, but differs in its larger size and fewer locules.

DISTRIBUTION AND AGE. Known only from the type locality (Early-Late Oligocene).

AFFINITY. With *Elaeocarpus*, possibly *E. stellaris* L.S.Smith, fruits of which are typically 5-loculate, rarely 7-loculate (Rozefelds & Christophel, 1996a).

Elaeocarpus spackmaniorum Rozefelds, 1990
(Figs 19A-M, 20A-F)

MATERIAL. HOLOTYPE (by original designation) QMF15440 (Fig. 19A-C) from ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Permineralised 5-loculate inner mesocarp, spheroidal, vertical and lateral axes 12.5mm. Five longitudinal sutures extend from base to apex and delimit 5 segments that have prominent sculpture of verrucae and rugulae up to 1x3mm in basal diameter and 0.5-1mm high.

DESCRIPTION. Fruit stones spheroidal, vertical and transverse axes 8-13.5mm with 5 or, more rarely, 3-4 locules and segments, the latter delimited by longitudinal sutures. Inner mesocarp wall 1.2-2mm thick, composed of compact isodiametric cells; sculpted externally with verrucae, bacula, and rugulae; sculptural elements up to 1mm high, 1mm wide and 2-4mm long. Locules equally developed or the seedless locules compressed; thin endocarp with tangentially oriented elongate cells and hollow central axis represented in sectioned specimens. Seed cavity ovoid,

FIG. 17. *Elaeocarpus pleioclinis* (F.Muell.) comb. nov., fruit stones and seeds. A-D, lectotype comprising two segments of original 8-locular fruit stone (NMVP53747, see Mueller, 1873, pl. VI, figs 3, 4). A, lateral view of two segments showing inner and outer surfaces, × 3. B, external surface of segment on right in A, × 3. C, detail of apical part of segment on right in A, × 4. D, Mueller's (1873, pl. VI, figs 3, 4) illustration of lectotype, × 1.5; E, Mueller's (1873, pl. IV, figs 1, 2) illustration of another specimen in apical and lateral view, × 1.5. F, G, lateral view of F, external and G, interior surface, × 3. H, apical, × 3, and I, lateral, × 2, views of specimen. J, spherical sclereids with pitted walls underlying elongate sclereids of outer epidermis of tegmen, × 250. K, detail of spherical sclereids, × 750. L, detail of elongated sclereids with thickened, pitted walls forming outer epidermis of tegmen, × 750. M, outer cuticle of testa, × 750.
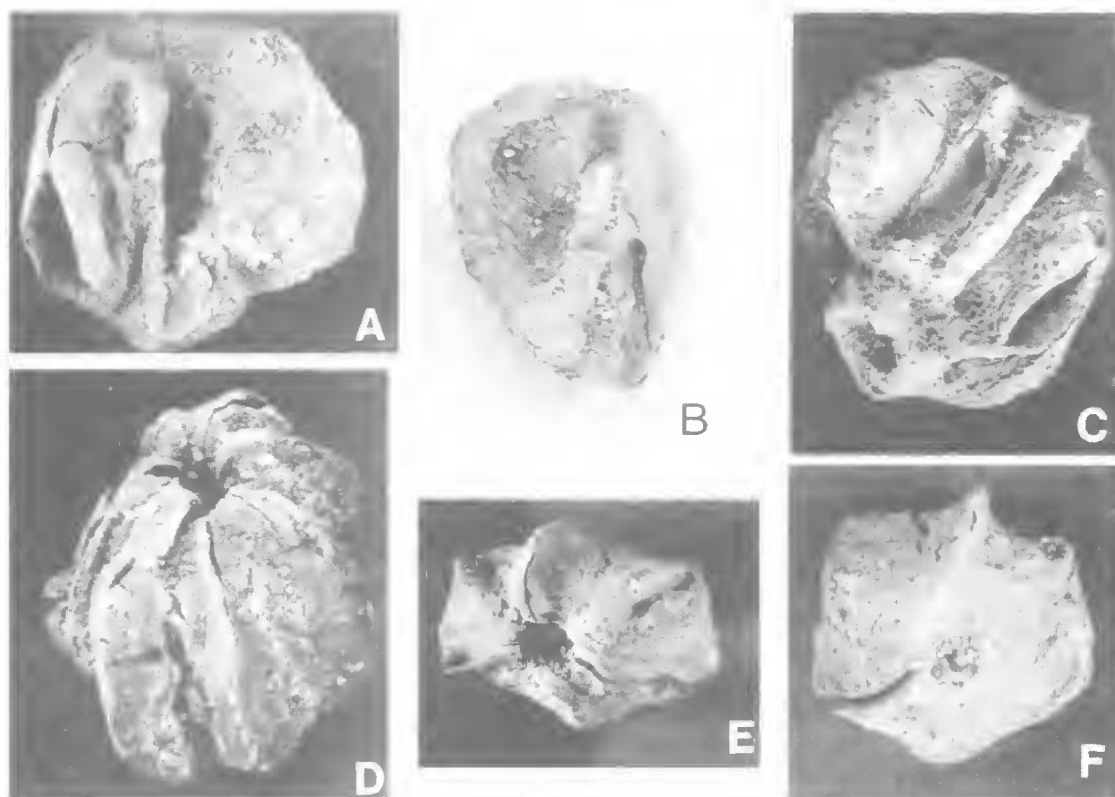
FIG. 18. *Elaeocarpus rozefeldsii* sp. nov. fruit stones. A,C, holotype, × 2, QMF50123 showing externally concave segments and seed cavity; A, lateral view; C, oblique view. B, internal view of segment, × 2, showing seed cavity. D, oblique apical view of larger specimen, × 2. E-F, another specimen, × 2; E, apical view; F, basal view.

up to 9mm long, 4mm wide. Seed with near apical attachment, ovoid; seed coat bitegmic.

REMARKS. In their amplified description of the species Rozefelds & Christophel (in press) note an exocarp and outer mesoearp on one specimen, thus corroborating identity with *Elaeocarpus*; fibre bases occur on the outer surface of the inner mesocarp in some specimens (Fig. 19J). A permineralised specimen transversely sectioned displays equally developed locules, but another specimen from the same locality shows a single seed bearing locule with the other locules compressed (Fig. 19K-M).

COMPARISON. *E. mackayi* is spheroidal with similar sculptural attributes and intergrades with 3-loculate specimens of *E. spackmaniorum*. *E. couchmanii* has a greater number (7-9) of locules and has fossulate sculpture. *E. trachyclinis* has rugulate sculpture and is considerably larger (~30mm in diameter).

DISTRIBUTION. Glencoe near Capella, Picardy Station near Moranbah, Hole RDPD998MA 17at 111-133m, Qld; Guildford, Vic. (Rozefelds, 1990; Rozefelds & Christophel, in press).

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. Resemblance to *E. angustifolius* Blume was emphasised by Rozefelds (1990) and Rozefelds & Christophel (1996a, in press), but fruit stones of extant species are usually larger.

Elaeocarpus trachyclinis (F.Muell.) Selling, 1950
(Fig. 21A-I)

Pentenne trachyclinis F.Muell. 1874a: 41, pl.8, figs.10-17.
Elaeocarpus trachyclinis (F.Muell.) Selling 1950: 559.

MATERIAL. LECTOTYPE (here designated): NMV53758 (Mueller 1874a, pl. 8, fig. 10, 11; Fig. 21D-G) from ?Early-Middle Miocene at ~47.5m in Reform Co Shafy, Smythe's Ck, Haddon, Victoria. Two fragmented segments of a partially pyritised woody inner mesocarp that was originally 5-loculate and near spheroidal, vertical axis 30mm and the transverse axes 32mm. Segments
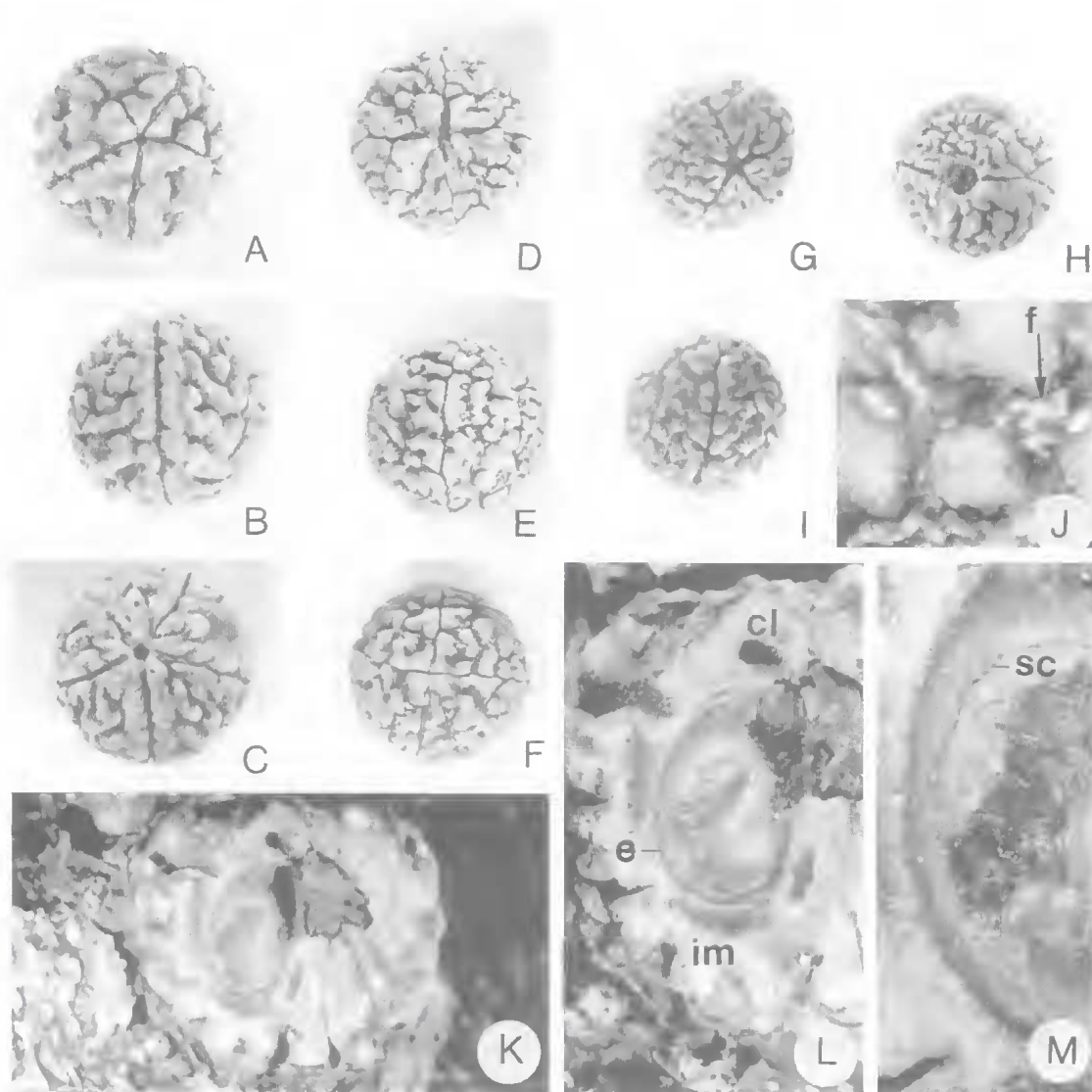
FIG. 19. *Elaeocarpus spackmaniorum* Rozefelds, permineralised fruit stones. A-C, holotype (QMF15440, see Rozefelds, 1990, fig. 4 A,B), × 2; A, apical view; B, lateral view; C, basal view. D-F, paratype (QMF15442, see Rozefelds, fig. 5 A,B), × 2; D, apical view; E, lateral view; F, basal view. G-I, paratype (QMF15444, see Rozefelds, 1990, fig. 4G), × 2; G, apical view; H, basal view; I, lateral view. J, surface detail of inner mesocarp and fibres (f) preserved on surface, × 16. K-M, oblique transverse section of fruit stone with one seed-bearing locule and two compressed locules (cl); note endocarp wall (e), seed coat (sc) and irregularly crested sculptural elements on the surface of the inner mesocarp; J, × 6, K, × 4, L-M × 16.

convex externally, with rugulate sculpture. One locule with an ovoid seed cavity 5mm wide and 14mm long, the other compressed; mesocarp wall 5mm thick, with many transverse cracks; endocarp not preserved.

DESCRIPTION. Fruit stones spheroidal or ellipsoidal when compressed, the vertical axis 32-36mm and transverse axes 25-35mm; sculpted externally by rugulae, with 5 evenly spaced longitudinal sutures. Fruits 5-loculate, 1 or more containing a single near apical seed, other locules sterile and compressed. Mesocarp 5-6mm thick, sculpted with rugulae (1mm wide, up to 6mm long) orientated near parallel to the vertical axis in well-preserved material; in abraded specimens sculpture much reduced.
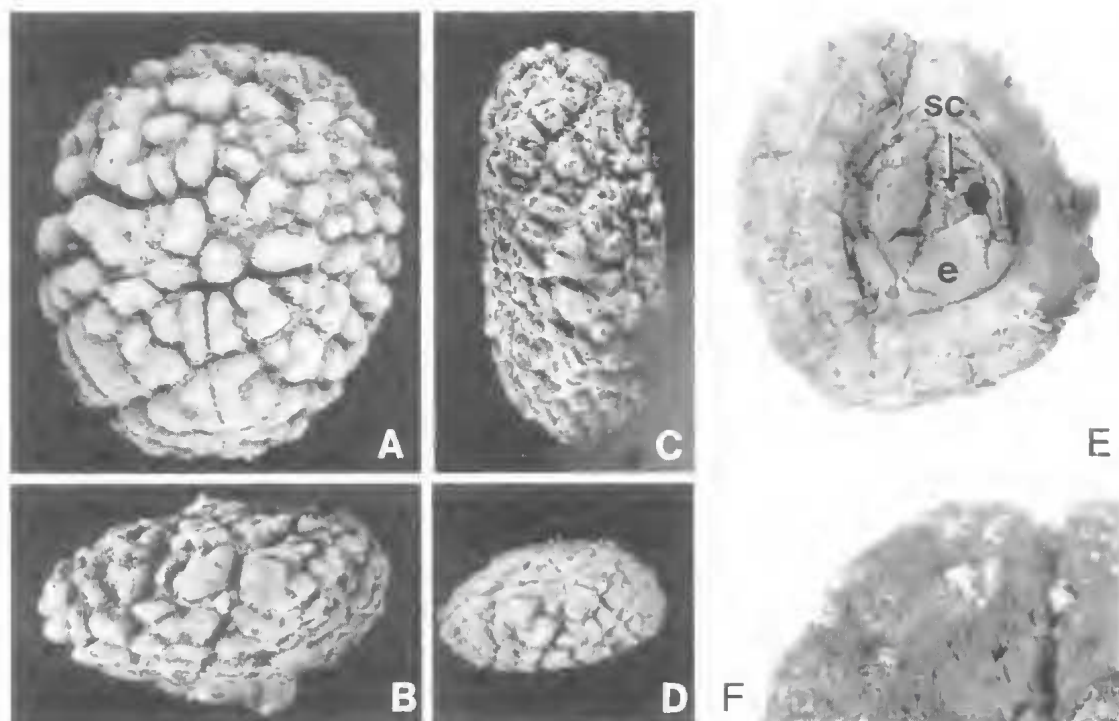
FIG. 20. *Elaeocarpus spackmaniorum* Rozefelds, charcoalfied fruit stones and seeds. A-D, compressed specimen, × 2; A, C, lateral views; B, D, apical views. E, F, internal surface of segment; E, seed-bearing locule with endocarp (e) and seed coat (sc), × 4; F, detail of inner mesocarp × 10.

Endocarp wall thin, enclosing ovoid locules with seed cavity 18mm long, 12mm wide.

REMARKS. The species was based on segments of 2 charcoalified, partially pyritised specimens.

COMPARISON. Similar in sculpture to *E. lynchii* which however is perprolate.

DISTRIBUTION. Haddon (Smythe's Creek, Reform Co Shaft, ~47.5m; Nintingbool, Crucible Co. Shaft, 23.2m), Beechworth (Eldorado), Victoria (Mueller 1874b, Mueller 1875); Risdon, Tasmania (Johnston, 1882); Bethany, South Australia (Hossfeld, 1949).

AGE RANGE. Oligocene-Miocene.

TAXON QUESTIONABLY ATTRIBUTABLE TO *ELAEOCARPUS*

Rhytidotheca major Deane, 1925

Rhytidotheca major Deane, 1925: 491, pl. LX, fig. 12 (nomen nudum).

REMARKS. The single specimen from Foster, Victoria figured by Deane (1925: 491) is said to be 'portion of a valve of a fruit like a large *Rhytidotheca*', but no description was provided

and the name is thus a nomen nudum (Greuter et al., 1994, Art. 32).

FOSSIL FRUIT TYPES OF *ELAEOCARPUS* AND THEIR DISTRIBUTION IN TIME AND SPACE

Fossil fruit stones of *Elaeocarpus* display a greater morphological range than that detailed for extant Australian and New Zealand species. However, it has been demonstrated that several of the fossil taxa have near congruence with fruit stones of extant Australian species. For example, fossil fruit stones *E. cerebriformis* differ only in size from those of *Elaeocarpus* sp.1 (Coode, 1984)/ *E.* sp. (Mossman Bluff, Henderson, 1997). Fossil stones of *E. clarkei* and *E. peterii* are similar in size, shape and inner mesocarp surface sculpture to fruit stones of extant *E. baucroftii* and *E. stellaris,* respectively, but differ in locule number. Rozefelds & Christophel (1996a, b) concluded that surface sculpture and shape of the fruit stone has potential for assessing affinites between fossil and extant taxa. Their 7 sculptural types provided the basis for delineating species groups among extant and fossil fruit stones of
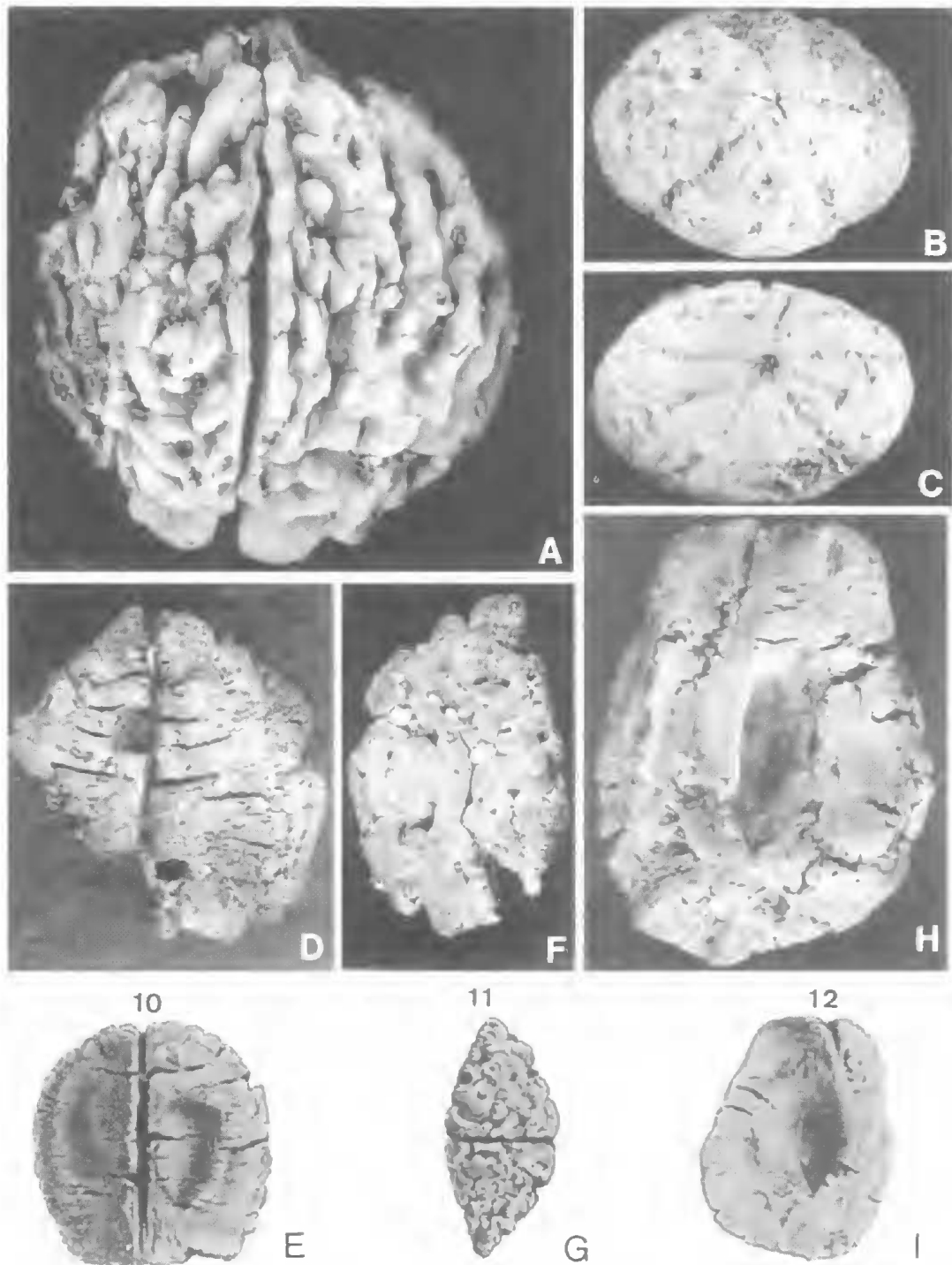
FIG. 21. *Elaeocarpus trachyclinis* (F.Muell.) Selling, fruit stones. Well preserved specimen consisting of two segments, × 2; A, lateral view; B,C, apical and basal views of abraded specimen. D-G, lectotype comprising two segments that are abraded of original fruit stone, NMV53758. D, internal surfaces of two segments; F, external view of one segment; E, G as illustrated in reverse by Mueller (1874a, pl. VIII, figs 10, 11), × ~1. 11, I, internal surface of fruit stone, × 2; H,seed cavity; I, as illustrated in reverse by Mueller (1874a, pl. VIII, fig.12), × ~1.

TABLE 2. The fossil and extant Australian and New Zealand species of *Elaeocarpus* grouped into five stone-types on the basis of the sculptural attributes of their inner mesocarps as defined. To facilitate comparison the ornamentation types of Rozefelds & Christophel (1996b) are given in parentheses. Extant species as listed in Hnatiuk (1990). * Coode, 1984; Henderson, 1997.

Stone type	Sculptural attributes	Fossil taxa	Extant taxa
Type 1	Surface with raised sculpture; basal diameter of elements (usually high relief bacula, verrucae and/or rugulae): transverse diameter of fruit stone > 0.1 (baculate, bastionate, verrucate, echinate in part)	*E. cerebriformis, E. cunningii, E. johnstonii, E. mackayi, E. muelleri, E. spackmaniorum*	*E. angustifolius, E. arnhemicus, E. carolinae, E. coorangooloo, E. culminicola, E. eumundi, E. holopetalus, E. kirtonii, E. obovatus, E. reticulatus, E. ruminatus, E. williamsianus, E. sp. nov. 1**
Type 2	Surface with raised sculpture; basal diameter of elements (usually low relief verrucae, rugulae, grana): transverse diameter of fruit stone < 0.1 (echinate in part, granulate)	*E lynchii, E. trachyclinis*	*E. costatus, E. dentatus, E. elliffii, E. hookerianus, E. grahamii, E. sericopetalus*
Type 3	Surface with pits or foveolae (punctate)	*E. allportii, E. brachyclinis, E. clarkei, E. peterii, E. rozefeldsii(?)*	*E. bancroftii, E. linsmithii, E.stellaris*
Type 4	Surface smooth or near smooth (smooth)	*E. angulare, E. bivalve, E. pleioclinis*	*E. ferruginiflorus, E. foveolatus, E. largiflorens, E. johnsonii, E. thelmae*
Type 5	Surface with fossulae	*E. couchmanii*	Not known

from Australia and New Zealand (Rozefelds & Christophel, 1996b); neither shape of the fruit stone nor locule number was utilized in their classification. Three of the categories – smooth, punctate and granulose – are well characterised, but mild abrasion of granulose fruit stones may reduce the sculpture to smooth and thus far fossil fruit stones having granulose sculpture remain unrecorded. Moreover, sculptural types distinguished as 'verrucate', 'echinate', 'baculate', and 'bastionate' (Rozefelds & Christophel, 1996b, table 2) may be difficult to uphold as exemplified by *E. angustifolius* whose fruit stone sculpture is said to be bastionate. The sculpture comprises a mix of bacula (straight-sided, flat crested elements), echinae (tapering, pointed processes), and distally expanded processes with flat, pointed or rounded crests, and these elements may be coalesced to form rugulae (Figs 5, 6). Furthermore, they described the fruit stones of *E. reticulatus* as echinate, but the elements include both round-topped (verrucae) and pointed (echinae) processes (Fig. 7).

Sculptural elements, particularly the distal crests of raised elements, may be substantially modified from their original form by abrasion during transportation. Even so, the bases of elements are likely to be preserved in all but extremely abraded fruit stones. The alternative grouping proposed here for stones with raised sculpture is based on the basal diameter of the sculptural elements relative to the transverse diameter of the fruit stone (Table 2). Many of the fossil taxa with raised sculpture included within Types 1 and 2 have sculptural patterns composed of a mix of bacula, verrucae, echinae and rugulae,

and each includes the baculate, bastionate, echinate and verrucate ornamentation classes of Rozefelds & Christophel (1996b, table 2). Types 3 and 4 accommodate taxa with punctate and smooth fruit stones respectively and Type 5 includes taxa with fossulate sculpture, a sculptural type not represented among extant Australian and New Zealand species (Table 2).

The fruit stone fossil record confirms that *Elaeocarpus* in eastern Australia dates to at least the Early Oligocene (Fig. 22) and corroborates evidence from cuticles and leaves (Carpenter, 1994). There are older (Eocene) records of leaves and cuticle of Elaeocarpaceae (*Elaeocarpus* or *Sloanea*) and of *Elaeocarpus*-like pollen from eastern Australia, but these await detailed systematic resolution (Truswell et al., 1987; Rowett, 1991; Rowett & Sparrow, 1994; Christophel, 1994). A Late Paleocene, leaf/cuticle record of the family is known from Cambalong Creek, Victoria (Valdala & Greenwood, in press). Thus far, reliable fossil records of fruits/leaves of Elaeocarpaceae indicate a geographic range from southernmost Tasmania north to central Queensland and west to southern South Australia. A range to northern South Australia may be implied by Late Paleocene-Early Eocene pollen (Martin, 1998). This distribution varies from its present range insofar as *Elaeocarpus* is no longer represented in South Australia or Tasmania. In New Zealand the Elaeocarpaceae has a history extending to at least the early Miocene as attested by leaves (Pole, 1993, 1996), but indubitable fossil fruits of *Elaeocarpus* are thus far unreported from pre-Quaternary sediments.

SERIES EPOCHS / FRUIT TYPE	QUEENSLAND					NEW SOUTH WALES					VICTORIA					TASMANIA					SOUTH AUSTRALIA					NEW ZEALAND				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Present-day	■	■	■	■		■	■				■					■										■				
Pleistocene																										■				
Pliocene																														
Miocene																													?	
Oligocene																														
Eocene																														
Paleocene																														

FIG. 22. Recorded distribution and stratigraphic range of *Elaeocarpus* fruit stone types as defined in Table 2. Broken lines indicate age uncertainties of sediments; ? indicates uncertain record.

Not only has the genus distribution changed in Australia since the mid-Tertiary, so too have the distributions of species groups that shed the individual stone types (Table 2). Today species with Type 1 fruit stones are distributed from northernmost Tasmania to N Queensland, but during the mid-Tetiary ranged westward into S South Australia (Fig. 22). Type 2 fruit stones are shed by taxa that today occur in NSW (Lord Howe Island), Queensland and NZ in contrast to their more southerly and westerly mid-Tertiary distribution range of Victoria, NSW and South Australia. Extant species that have pitted fruit stones (Type 3) are restricted to N Queensland and NT, whereas during the mid-Tertiary this type had an E Australian distribution from S Tasmania to central Queensland. The mid-Tertiary distribution of smooth stones (Type 4) included Victoria and NSW, whereas today taxa with smooth stones are restricted to Queensland and regions to the north (Fig. 22). The record also implies a former higher species diversity in the region. Type 5 stones, without living counterpart in Australia, are present in Tertiary sediments of Victoria, NSW and South Australia (Fig. 22).

ACKNOWLEDGEMENTS

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APPENDIX 1: Register of figured specimens. * denotes nomenclatural type.

Taxon.	Fig. No.	Original Figure	Specimen Status	Locality	Repository. Reg. No.
E. angularis	8A-F	Mueller, 1874c, pl. X, figs 1-4	Holotype *	Haddon (Smythe's Ck), Vic	NMVP53565,6017
E. bivalve	9A-C		Neotype *	Black lead, Gulgong, NSW	MMF36220
	9D-G		-	Forest reefs, Gulgong, NSW	AMF6669
	9H,I		-	Black lead, Gulgong, NSW	MMF36221
	9J-K		-	Forest reefs, Gulgong, NSW	AMF6669
E. brachvelinis	10A-C	Mueller, 1874a, pl. VIII, fig. 4	Lectotype *	Haddon (Synthe's Ck), Vic	NMVP6060
	10E-G,I		-	Haddon. Vic	NMVP212639
	10H		-	Haddon. Vic	NMVP6025
	10J-L		-	Haddon, Vic	NMVP53918
E. clarkei	11A,B	Rozefelds & Christophel, 1996a, pl. 1, figs A-C	Neotype *	Elsmore, NSW	AMF9281
	11C-I		-	Victory Mine, Orange. NSW	AMF8440
E. conchmanii	12A-C	Mueller, 1882, pl XIX, figs 3,11	Lectotype *	Haddon (Nintingbool), Vic	NMVP53920
	12E-G		-	Haddon. Vic	NMVP53921
E. cuningii	13A-D	Rozefelds. 1990, fig. 6D	Holotype *	Glencoe, Capella, Qld	QMF16768
	13E,F,G			Picardy Station, Moranbah. Qld	QMF50114
	13H	Rozefelds 1990, fig. 6E	Paratype	Glencoe, Capella, Qld	QMF50115
	13I,J			Glencoe, Capella, Qld	QMF50116
	13K			Glencoe, Capella, Qld	QMF50117
	13L			Glencoe. Capella, Qld	QMF50118
E. lynchii	14A-C	Mueller 1871b, pl. IV, figs 1-4	Lectotype * (2 segments)	Haddon (Nintingbool), Vic	NMVP6034
			Lectotype * (1 segment)	Haddon (Nintingbool) Vic	NMVP6035
	14I-K			Haddon, Vic	NMVP53969
	14L-O			Smythsdale. Vic	QMF50119
E. mackayii	15A,B,I	Mueller, 1871a, pl. II, fig. 4; Rozefelds & Christophel, in press, fig. 2A,B	Lectotype *	Haddon (Smythe's Creek), Vic	NMVP53562
	15C			South Blackwater, Qld	QMF50120
	15D			Picardy Station, Moranbah, Qld	QMF50121
	15E-G			Picardy Station, Moranbah. Qld	QMF50122
	15H			Picardy Station, Morandah. Qld	QMF51078
E. peterii	16A-D	Rozefelds & Christophel, 1996b, pl. 3. figs A,C,E,G,I	Holotype *	Glencoe, Capella. Qld	QMF18088
E. pleioclinis	17A-C	Mueller, 1873, pl. VI, figs 3,4	Lectotype *	Haddon (Nintingbool), Vic	NMVP53747
	17F,G			Haddon, Vic	NMVP53741
	17H,I			Haddon, Vic	NMVP53741
	17J-M			Haddon. Vic	NMVP53741
E. rozefeldxii	18A,C	Mueller, 1873, pl. VI, figs 3,4	Holotype *	South Blackwater, Qld	QMF50123
	18B			South Blackwater, Qld	QMF50124
	18D			South Blackwater, Qld	QMF50125
	18E,F			South Blackwater, Qld	QMF50126
E. spackmaniorum	19A-C	Rozefelds, 1990, figs 4A,B	Holotype *	Glencoe, Capella. Qld	QMF15440
	19D-F,J	Rozefelds, 1990, figs 4E,F	Paratype	Glencoe, Capella, Qld	QMF15442
	19G-I	Rozefelds, 1990, fig. 4G	Paratype	Glencoe, Capella. Qld	QMF15444
	19K-M			Glencoe, Capella, Qld	QMF50127
	20A-D			Picardy Station, Morandah, Qld	QMF51076
	20E-J			Picardy Station, Morandah. Qld	QMF51077
E. trachyelinis	21A			Haddon. Vic	NMVP53984
	21B,C			Haddon (Smythe's Creek) Vic	NMVP53922
	21D,E	Mueller, 1874a, pl. VIII, figs 10,11	Lectotype *	Haddon, Vic	NMVP53758